# *SOLANUM NIGRUM* L. (SOLANACEAE) AND RELATED SPECIES IN AUSTRALIA


## SUMMARY

Plants previously known as *Solanum nigrum* in Australia are *S. opacum* A.Br. & Bouché (2n = 72) and *S. nodiflorum* Jacq. subsp. *nutans* R. J. Henderson *subsp. nov.* (2n = 24) which are considered native, and the naturalized *S. nigrum* L. subsp. *nigrum* (2n = 72) and subsp. *schultesii* (Opiz) Wessely (2n = 72), *S. nodiflorum* Jacq. subsp. *nodiflorum* (2n = 24), *S. gracilius* Herter (2n = 24), *S. nitidibaccatum* Bitt. (2n = 24) and *S. villosum* Mill. (2n = 48). *S. furcatum* Dun. (2n = 72) and *S. retroflexum* Dun. (2n = 48) are also naturalized to a very minor extent. *S. scabrum* Mill. (*S. melanocerasum* All. *syn. nov.*) (2n = 72) and *S. douglasii* Dun. (2n = 24) have been grown occasionally though neither has been found naturalized. A form of *S. nodiflorum* subsp. *nodiflorum* grown from seed from U.S.S.R. is hexaploid (2n = 72).

A key for the identification of 11 species of *Solanum* sect. *Solanum* native to or naturalized in Australia is given. With the exception of the excluded *S. triflorum* Nutt., each of these species is described and its distribution in Australia based on herbarium specimens, is mapped.

Cross-breeding data help to explain anomalies observed in pollen viability counts. All included species are principally self-pollinating. F1 progeny of *S. nodiflorum* subsp. *nodiflorum* x subsp. *nutans* is 18–25% pollen fertile, F2 is 0–99% pollen fertile. *S. nodiflorum* subsp. *nutans* and *S. opacum* are genetically isolated by hybrid inviability.


## INTRODUCTION AND ACKNOWLEDGEMENTS

Taxonomy and nomenclature of the group of species related to and including *Solanum nigrum* L. have been the subject of extensive study throughout the world, e.g. North America (Stebbins & Paddock, 1949), Costa Rica (Heiser, 1955, 1965), South America (Gray, 1968; Edmonds, 1972), Europe (Jorgensen, 1928; Wessely, 1960), Japan and Taiwan (Nakamura, 1935, 1937), India (Tandon & Rao, 1964, 1966), New Zealand (Baylis, 1958) and Australia (Cheel, 1917). Some authors e.g. Dunal (1852) and Bitter (1911 et seq., see Edmonds for further references) have recognized very many species in the group while others e.g. Bentham (1869) and Hitchcock et al. (1959) have maintained that there is but one highly variable species namely *S. nigrum*. The actual situation seems somewhat between these extremes.

Though Baylis had studied some Australian plants and made some comment on their identity, the situation regarding forms near Brisbane was not fully clarified by his conclusions. Cheel's account of the group seems the most recent work on Australian plants but in the light of extensive field experience proves most unsatisfactory. A detailed study of the plants in Australia has been undertaken and the conclusions are now presented.

This paper is the result of about ten years intermittent study based on extensive field observation of wild and naturalised plants mainly in Queensland and to a small extent in South Australia, on plants grown in a glasshouse from seed from Australia and from New Zealand, U.S.A. and U.S.S.R., on fresh and fixed material studied in the laboratory and examination of several hundred dried herbarium specimens.

Those in the Queensland Herbarium (BRI) provided a sound basis for the study. This was consolidated by study of herbarium material obtained on loan through the courtesy of the Directors of the following herbaria: A, AD, ADW, BM, CANB, CHR, GFW, IND, K, MEL, NSW, PERTH and UC. Symbols for herbaria throughout are those listed in Index Herbariorum, Reg. Veg. 31:1964.

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## CITATIONS

References to literature in the text have been restricted to protologues and others requiring comment in relation to Australian plants. All collections cited have been examined unless marked "not seen". The method of citation of microfiche of specimens is that proposed by Hepper (1968). References to ICBN are to the International Code of Botanical Nomenclature (1972). Extensive reference has been made to Stafleu (1967) in establishing date of publication of species names.

## SCOPE OF STUDY

This study has been limited to the somewhat natural group of species centred on *Solanum nigrum,* as it occurs in Australia. These species with *S. triflorum* Nutt. represent here *Solanum* sect. *Solanum* (sens. Seithe, 1962) members of which may be described as follows.

Herbs shrubs or subshrubs, without pungent prickles or stiff spines, rhizomes stolons or root shoots never present; pubescence where present of soft multicellular hairs; hairs simple or rarely once-branched, never stellate, the apical cell sometimes glandular; leaves herbaceous, entire sinuately-lobed pinnatifid pinnatisect or bi-pinnatisect. Inflorescences pedunculate with one to twelve flowers, mono- or dichasial; flowers less than 2 cm diameter, white or tinged with purple or rarely wholly violet; corolla stellate or rotate, lobes 5(–8); calyx lobes 5(–8); anthers in outline narrow ellipsoidal or oblong, of ± uniform width; filaments usually with spreading multicellular acute or sometimes glandular hairs; style with short spreading hairs or papillae in the lower regions; stigma globular, capitate. Fruit a succulent, bilocular or rarely trilocular, many-seeded berry.

*S. triflorum* is considered to be not closely related to the "Morella" group (see also Dunal (1852) who placed it in a separate grouping within his Subsection Morella) and is therefore not dealt with formally in this paper though included in the key to species.

## DIAGNOSTIC CHARACTERS

The following attributes were examined in a search for characters useful for diagnostic purposes in the group:

### HABIT AND LIFE HISTORY

In all species except *S. opacum,* plants are usually erect or ascending though at times become procumbent. Plants of *S. opacum* are usually procumbent or even prostrate, though in early stages of growth can also be erect. Branches of *S. gracilius* and *S. furcatum* may be long and weak, the plants then becoming sprawling or decumbent. Some species persist for only a few months (*S. nitidibaccatum*), others for as long as a year or eighteen months or with repeated pruning from four to five years (*S. nodiflorum*). Flowering can commence as little as two weeks after emergence of the seedling and continue uninterrupted for the remainder of the life of the plant. Flowering plants may be from as little as 3 cm (*S. nigrum*) to about 1·5 m tall (*S. nodiflorum*). Prostrate plants of *S. opacum* can be up to about 1 m in diameter.

The form of a plant is also dependent on its age. Senescence is associated generally with twisted woody stems, small leaves and fewer smaller flowers and fruits than is usual for the species. Plants developing from seed germinating on the surface of the soil often have an atypical sprawling habit when they develop under unfavourable conditions.

Factors in the environment can alter greatly the morphological aspect of a plant. Since they are generally treated as weeds, plants rarely reach the fully mature stage of development. They are frequently disfigured by mowing or malformed by application of phenoxy herbicides. Browsing stock can alter appreciably the appearance of plants. Leaf-eating insects e.g. the 28-spot Ladybird (*Henosephilachna vigintioctopunctata* (F.)), the Large Leaf-eating Ladybird (*H. guttapustulata* (F.)) and adult Potato Flea Beetles (*Xenidia picticornis* Blackb.), produce disfiguring effects on plants of *S. nodiflorum* and are thought to be responsible for rare monstrosities as a result of breakdown of apical dominance in the vegetative shoot. Viral infection occasionally produces leaf malformations including complete suppression of blade development.

## INDUMENTUM

Characters of the indumentum are diagnostically useful but mainly of secondary importance. In all species, simple uniseriate hairs and minute stipitate multicellular glands compose the indumentum of stems, leaves, and most parts of the inflorescences. Widely spaced erect simple hairs, prickle hairs (as defined by Roe, 1971) or modified prickle hairs (pricklets) occur on the ridges on stems in some species. Uniseriate hairs are either widespreading or somewhat antrorsely curved, in some species even strongly curved but never strictly appressed. Though predominantly simple, occasional once-branched hairs occur on some leaves of *S. gracilius* and *S. douglasii*. Spreading types are glandular or eglandular but strongly curved types are always eglandular. Glandular hairs have the single apical cell expanded and ± globular in shape. The apex of the inconspicuous stipitate glands consists of a number of cells (usually 4) placed laterally, the group somewhat depressed globular in outline (cf. Seithe, 1962, T.25, 1–3, 7–8). Numerous widespreading hairs tend to give the plant an almost shaggy appearance (e.g. *S. villosum* and *S. nitidibaccatum*) while dense, mainly strongly curved hairs give plant parts a sub-velvety aspect (e.g. *S. gracilius*). The densities of these superficial epidermal structures vary independently, yet each is influenced by such factors as the species to which a plant belongs, the organ under consideration and its age relative to that of the plant as a whole as well as environmental conditions during its growth. Hairs may be from thickly matted to almost completely lacking. Glands though often relatively dense on younger vegetative parts, become more widely spaced with expansion of the maturing organ.

## STEMS AND LEAVES

The presence or absence of ridges or "wings" on stems and the presence or absence of short soft protruberances or prickle hairs ("teeth" or "spines" of some authors) on these ridges, are not considered of the diagnostic importance attributed to them by Dunal and certain other authors. Though generally more prevalent in certain species (e.g. *S. nodiflorum* and *S. furcatum*) the degree of

development of these features has been found to vary between individuals of the one species depending on where the plant was growing and the conditions under which it was grown. Similar variation has been noted on the same plant at different stages throughout its growth cycle. The ridges or wings are an expression of decurrent leaves and the prickle hairs that occur on them are therefore probably homologous with leaf lobes.

Absolute size of leaf blades and petioles varies considerably within a species (e.g. blades 2–18 cm long in *S. nodiflorum*). The shape of the leaf blade varies within a broad though characteristic range for each species but these ranges tend to overlap. The margin of the leaf blade has been used as a diagnostically important feature by some authors. Some species with adult leaves more or less entire or somewhat sinuate (e.g. *S. nodiflorum* subsp. *nodiflorum*) can have leaves quite deeply and regularly indented on seedlings or coppice shoots from damaged adults. Conversely, entire leaves can occasionally be found on plants in which adult leaves are usually indented.

In all species except *S. opacum* the teeth on the leaf-margins are obtuse and usually forwardly directed or occasionally even spreading perpendicularly to the midrib. With *S. opacum,* lobes where present, are prominent, acute and almost always spreading at a wide angle to the midrib (Plate 6 (A)).

### INFLORESCENCE AND INFRUCTESCENCE

In all species, flowers are borne in an extra-axillary cincinnal cyme which has undergone degrees of condensation characteristic of the particular species concerned. Where pedicels are relatively numerous and condensation least, inflorescences and infructescences appear racemiform (e.g. Plate 7 (K)). Where reduction in the number of pedicels occurs together with extreme condensation of the axis, inflorescences and infructescences appear umbelliform (e.g. Plate 7 (I)). True umbels do not occur in any of the species.

Orientation of the peduncle of infructescences relative to its supporting stem and that of the pedicels relative to the peduncle are manifestations of a geotropic response and hence are susceptible to realignment. With peduncles, erect or ascending types can appear reflexed when their supporting branches are bent downwards. Reflexed types become deflexed on horizontally spreading branches and are still directed downwards on pendulous branches e.g. in *S. opacum.* There seems therefore a genetic difference between species with negatively geotropic peduncles and ones with positively geotropic peduncles.

It is most likely that orientation of the pedicels is similarly under genetic control though due to genes different from those for peduncle orientation. Results of hybridization between subspecies of *S. nodiflorum* indicate that the different orientations of the pedicels are expression of different alleles of one gene.

Varying degrees of adnation of the peduncle with the stem results in internodal extra-axillary peduncles, the leaf-opposed or nodal state (e.g. sometimes in *S. nodiflorum*) representing the extreme.

Characteristics of the inflorescence are little effected by climatic environmental factors though heavy insect infestations or applications of phenoxy herbicides can produce misleading results.

### CALYX

The calyx of *S. nitidibaccatum* enlarges many times between flowering and fruiting and eventually embraces approximately half the fruit at maturity. In all other species, the calyx enlarges only slightly between flowering and fruiting at which time it may remain appressed to the berry, may spread at right angles to the pedicel or may become more or less strongly recurved or even strongly reflexed. More than one of these states can occur in one species.

### COROLLA

The corolla varies from approximately twice the size of the calyx to about five times its size. Pubescence on the outer surfaces varies considerably within each species. The lobes vary from narrowly semi-elliptic to ovate (in stellate corollas) to broadly triangular (in rotate corollas) and from about three times longer than the tube to a little shorter than it.

Though the corolla is often described as white, the central regions towards the base of each lobe, especially obvious on the inner surface, is a translucent greenish or yellowish colour. In some species each lobe may be marked towards the base, with a symmetrically placed pair of small purple spots which often coalesce with those on adjacent lobes to produce a series of V-shaped markings.

In *S. opacum, S. retroflexum* and possibly in some atypical plants of *S. nigrum* the length of the midline on the reverse of each white petal may be marked with deep purple producing a striped effect. In flowers of other species, the usually white corolla becomes suffused with variable amounts of violet-purple. Wholly violet-coloured flowers have been noted in *S. nodiflorum* and *S. douglasii*.

Development of these over-all colorations, no doubt due to anthocyanins, is probably as Baylis (1958) suggests, a dominant-recessive state Mendelian character governed by alleles of a small number of genes. However, natural environmental influences also affect expression of these genes. In the environs of Brisbane the presence of purple colorations especially in *S. nodiflorum* subsp. *nodiflorum* appears correlated with the relatively lower temperatures and lower levels of light intensity during winter.

The occasional striping occurring on the corolla of *S. opacum* is similarly under genetic control though perhaps attributable to a different gene, since presence or absence appears unaffected by environmental influences.

Opening of the corolla follows a definite series of stages from emergence from the bud till dropping following fertilization. At an early stage the lobes of all species spread till horizontal then rapidly become recurved to varying degrees (species with smaller flowers) or strongly reflexed (species with large flowers) after which they return to the style prior to dropping.

## STYLE AND STIGMA

The length of the style in relation to the ring of stamens connivent about it is of diagnostic importance. In some species (e.g. *S. furcatum* and *S. gracilius*) the style is long with the stigma consequently exserted 1–3 mm or sometimes more beyond the anthers. In others (e.g. *S. opacum* and *S. retroflexum*) the stigma may never emerge from the ring of anthers or if so remains approximately level with the pores of dehiscence. The relative position of stigma to pores of the anthers in the mature, fully open flower no doubt has a bearing on the breeding pattern of any particular species, a subject discussed later.

## STAMENS

The range of anther lengths though not unique to a species is most useful, in combination with other characters especially pollen size, for identification of plants. Climatic environmental factors seem to affect this range little but hybridism and insect attack can have a profound influence (see also under *S. nigrum*). Anthers on dried specimens tend to be fractionally shorter than they were when fresh. Measurements of anthers as used in the key to species refer principally to those in the dried state.

Except for *S. douglasii* variation in width of anthers within and between species is small (0·6–0·8 mm) and is considered insignificant. In *S. douglasii* anthers are up to ± 1·25 mm wide and tend to be broadest towards the base. With the exception of *S. villosum* variation in filament length is similarly considered insignificant. In that species anthers are at times shorter than the elongated filaments. Dehiscence of the anther is initially by apical pores which however soon become longitudinal slits of varying lengths in most species. Where the slit continues for the whole length, the anther appears broadest towards the tip (e.g. *S. opacum*).

## POLLEN

Range of sizes and stainability of the contents of pollen grains have been found useful diagnostic characters. Pollen is granular, hyaline, smooth and normally spherical in shape though prolate grains have been observed in some specimens, a condition previously encountered by other workers on *Solanum* pollen (Erdtman, 1952; Salaman, 1909; Sutton, 1909). In polar view, grains sometimes appear almost triangular or quadrangular in outline due to the slight protuberance of the three or occasionally four, equatorially placed germ pores. In equatorial view these grains can then appear elliptical in outline. Diameter measurements for the one grain, therefore, can vary depending on its position

when measured. Hence ranges in measurements of the grains, rather than average grain diameters are considered more meaningful taxonomically, though mean diameters serve as useful key characters.

All pollen observations were made with samples mounted in a mixture made to the formula 0·05 gm spirit soluble Aniline Blue (BDH Standard Stain), 50 ml lacto-phenol (BDH Microscopical Reagent) and 10 ml Glycerol (BP grade), using a Leitz 10/100 micrometer eyepiece calibrated to a W. Watson & Son 0·1/0·01 mm slide with Zernike phase contrast microscopy. Water was excluded as much as possible from the mounting media to reduce possible excessive swelling (Baylis, 1954). The viscosity of this mountant is such that light and/or abortive grains are less likely to float to the edges of the preparation. The possibility of misleading determinations of percentage of stainable grains is thereby reduced.

Percentage of stainable pollen has been taken as an indication of pollen viability but the exact correlationship between the two is not known, though methods of determining the actual fertility more accurately have been described (Alexander, 1969; Hauser & Morrison, 1964; Kaul & Singh, 1969).

It is considered that percentage of stainable grains in a pollen sample measured under standardized conditions is satisfactory for purposes of comparison and more practical to determine than actual fertilities especially on herbarium specimens of varying ages.

Grains of a collapsed or unstained appearance were taken to be sterile or inviable and were not included in grain size ranges. The presence of such grains in large quantities in pollen samples is considered an indication of hybrid origin, especially where the plants also show abnormalities or intergrading variation of leaf, inflorescence and fruit development. Plants with such intermediate characters but high pollen fertilities can be obtained amongst segregates from experimentally produced back- or out-crossed Fl hybrid individuals and in fact do occur in the field. Reduction in pollen fertility observed in otherwise apparently normal plants in this study and also noted in the literature (Baylis, 1958; Stebbins & Paddock, 1949), is not easily explained. The presence of such individuals may indicate development of incipient dioecism within a species. There appears to be no authenticated record of such a phenomenon in *Solanum* sect. *Solanum* though andro-monecism and andro-dioecism were recorded by Symon (1970) for a small group of native north-western Australian species referable to Section *Stellati-pilum*.

The presence of prolate grains is more prevalent in older specimens but age itself appears not to contribute directly to this condition. Preservational procedures would seem to have a more direct influence. Such grains have been observed in Australian material from forty to one hundred and thirty years old including specimens collected by Leichhardt between 1842 and 1847. They are also present in Miller's specimens (BM, Stearn per. comm.) collected in England during the eighteenth century. However, in a pollen sample from a specimen of *S. opacum*

collected possibly by Banks and Solander from Port Jackson, New South Wales in 1770 (NSW, BM) over 90% of grains were spherical and stained as if viable.

Pollen size is not directly proportional to chromosome number (Fig. 1) but when considered in conjunction with characters of the inflorescence allows for accurate prediction of ploidy level. Studies with Australian plants do not support the findings of Chennaveeraiah & Patil (1968) with Indian plants that size of pollen is almost the same at each ploidy level.

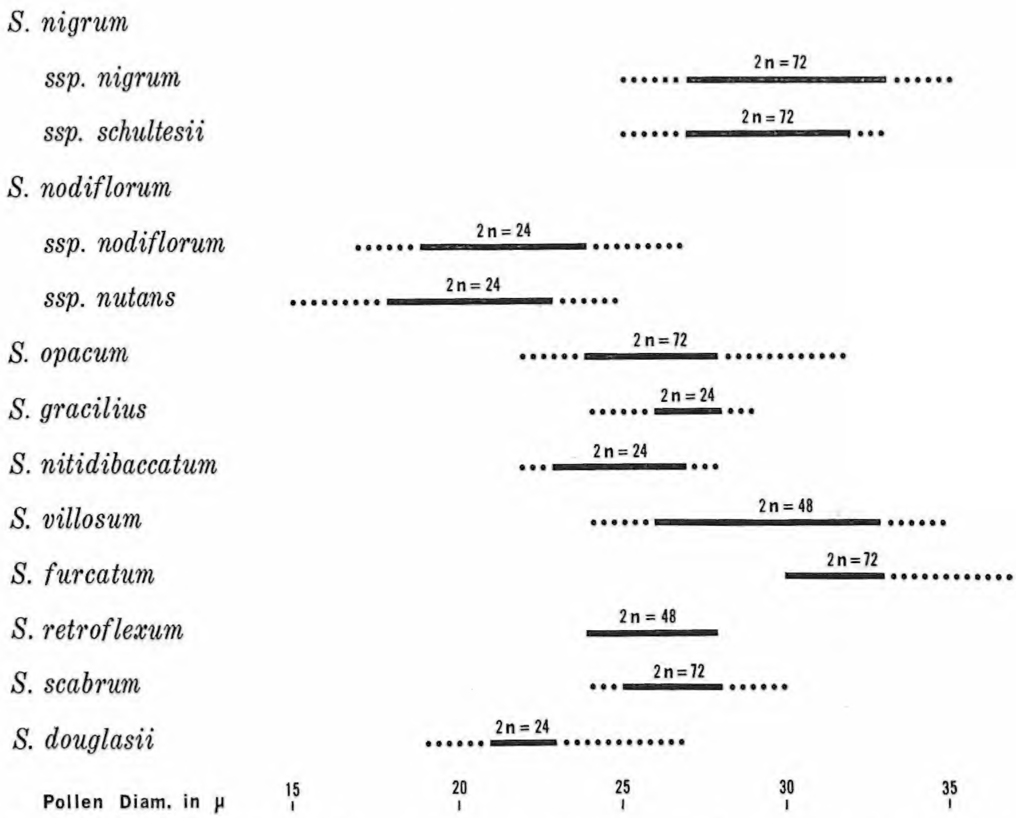


FIG. 1.—Comparison of the observed range of pollen sizes (in Lacto-phenol Aniline Blue) of certain species of *Solanum* sect. *Solanum,* with an indication of ploidy level in each.

## FRUIT

Mature berries are either depressed globular to spherical and green, purplish to black or longitudinally ellipsoid and bright to drab yellow to orange to red. These categories are considered mutually exclusive in spite of a small amount of conflicting evidence recorded in published accounts (see Wessely, 1960, p. 300) and from collectors notes on herbarium specimens (BRI 036136—specimen of *S. opacum* stated to have fruits red when ripe). According to Wessely, purplish to black colorations are due to anthocyanins while red to yellow hues result from the presence of flavones and carotenes.

The diameter of the berry in all species except *S. scabrum* is less than 1·2 cm. The cuticle of mature fruit is either shiny (lucid) or dull (matt) and is either opaque or sufficiently translucent to allow the seed to be easily seen. Stone-like sclerotic granules may be present or absent in the pulp though except in hybrids both states usually do not occur together in the one taxon. These granules are usually spherical and up to 1·5 mm across though size range is more or less characteristic of a species. They occur in pairs equatorially and/or at the apex, just beneath the epidermis but their exact position has yet to be determined in species in which they occur in numbers larger than eight.

Though these attributes of the fruit are probably most accurately determined in the living state, some are measurable in, and others suggested by, dried material or in extreme cases fruit reconstituted by boiling for about one minute in water.

### SEED

Seed is flattened and biconvex in section, cuneate at the base and obovate to obliquely obovate in outline, often within the one berry. The testa is rough from many parallel series of minute irregular pits. The length of the seed is approximately proportional to its breadth and varies to about 2·4 mm though each species has a more or less characteristic range. The number of seeds per berry while dependent to some extent on seed size, appears equally dependent on berry size. Berries resulting from cross-pollinations may contain no seed whatever or full-sized testas lacking embryos with or without some normal seed.

## CYTOLOGY

Somatic chromosome numbers of 24, 48 and 72 occur in plants of *Solanum* sect. *Solanum* in Australia (Table 1). This agrees with the findings of several workers on plants of the group in other regions of the world (e.g. Jorgensen, 1928; Nakamura, 1935, 1937; Stebbins & Paddock, 1949; Heiser, 1955, 1965; Baylis, 1958; Tandon & Rao, 1964, 1966; Gerasimenko & Reznikova, 1968; Zhukova, 1967; Edmonds, 1972).

For observation of chromosomes in this study, root-tip or pollen-mother-cell squashes were prepared from material collected from plants in the field or grown from seed under glasshouse conditions and fixed in standard 3:1 ethanol:glacial acetic acid mixture. Root tips were soaked in aqueous *p*-dichlorobenzene for about 2 hours prior to fixation. Preparations were stained in ethanol-hydrochloric acid-carmine according to the method of Snow (1963) or in aceto-carmine.

In all species, meiotic and mitotic chromosomes appeared principally as spherical spots, though in some species the centromere of some chromosomes of the complement was visible at late mitotic prophase. Chromosomes were not therefore able to be mapped, measured and characterized as Venkateswarlu and Bhiravamurty (1969) were able to do in what they called a diploid form of *S. nigrum* from India.

Chromosome behaviour at meiosis in artificially produced hybrids shows that a close relationship of homologous chromosomes exists between different species of the same ploidy level. In the great majority of cases bivalents only are formed, the only irregularities observed being failure of up to 4 chromosomes to synapse on rare occasions and formation of trivalents to an even less extent (see under *S. nodiflorum*). Where hybrids between plants of different ploidy level have been obtained their chromosome behaviour at meiosis has been most irregular and their pollen of a wide size range. Since some pairing has been observed in these meioses, chromosomes contributed by the parent with higher chromosome number are capable of pairing either autosyndetically as suggested by the work of Rai (1959) or with some chromosomes contributed by the second parent. Chromosomes of a gametic set in a diploid species seem incapable of autosyndesis since multivalent associations have never been observed in diploid meiosis.

TABLE 1

CHROMOSOME NUMBERS IN CERTAIN SPECIES OF *SOLANUM* SECT. *SOLANUM* IN AUSTRALIA

| Species | Origin of Material | Collector and Number | Chromosomes | | Voucher No. (BRI) |
|---|---|---|---|---|---|
| | | | n | 2n | |
| *S. nigrum* | | | | | |
| subsp. *nigrum* .. | Mt. Mee, Q. .. .. | *Henderson* 404 | 36 | | 140029 |
| | seed ex Mt. Mee, Q. .. | *Henderson* 404 | 36 | 72 | 082532<br>082553 |
| | seed ex Kentville, Q. .. | *Henderson* 123 | 36 | 72 | 062156<br>(parent) |
| | seed ex Hughenden, Q. .. | *Everist* 7291 .. | 36 | | 139112 |
| | seed ex Stanthorpe, Q. .. | *Bengston* .. | 36 | | 081221<br>090651 |
| | seed ex Mareeba, Q. .. | *Cunningham* .. | 36 | | 139115 |
| | seed ex Dunedin, N.Z. .. | *Baylis* .. .. | 36 | 72 | 081334 |
| | seed ex Moscow, U.S.S.R. | *Vilar Instit.* 1967 seed list 410 | 36 | 72 | 140038 |
| subsp. *schultesii* | seed ex Adelaide, S.A. .. | *Symon* 1944 .. | 36 | 72 | 139113 |
| *S. nodiflorum* | | | | | |
| subsp. *nodiflorum* | Salisbury, Brisbane, Q. .. | *Henderson* 299 | 12 | 24 | 073151 |
| | Domain, Brisbane, Q. .. | *Henderson* 260 | 12 | | 140043 |
| | Indooroopilly, Brisbane, Q. | *Henderson* 36 | 12 | | 039655 |
| | seed ex Moscow, U.S.S.R. | *Vilar Instit.* 1967 seed list 412 | 36 | 72 | 140032 |
| | seed ex Ecuador, S. Amer. | *Heiser* S.128 ex *Soria* | 12 | 24 | 081012 |

| Species | Origin of Material | Collector and Number | Chromosomes | | Voucher No. (BRI) |
|---|---|---|---|---|---|
| | | | n | 2n | |
| subsp. *nutans* .. | Salisbury, Brisbane, Q. .. | *Henderson* 298 | 12 | 24 | 073150 |
| | Indooroopilly, Brisbane, Q. | *Henderson* 518 | 12 | | 086633 |
| | 30 km S. of Warwick, Q. .. | *Henderson* 372 | 12 | | 081327 |
| | near Blackbutt, Q. .. | *Henderson* 280 | 12 | | 073133 |
| | near Blackbutt, Q. .. | *Henderson* 281 | 12 | | 073134 |
| *S. opacum* .. | near Blackbutt, Q. .. | *Henderson* 285 | 36 | | 073138 |
| | near Blackbutt, Q. .. | *Henderson* 290 | 36 | | 073142 |
| | Bunya Mts., Q. .. .. | *Henderson* 302 | 36 | | 134032 |
| | Wilsons Peak, Q. .. .. | *Henderson* 359 | 36 | | 134033 |
| | Mt. Mee, Q. .. .. | *Henderson* 403 | 36 | | 140028 |
| | Jolly's Lookout, Q. .. | *Henderson* 514 | 36 | 72 | 082999 |
| | seed ex Kenmore, Brisbane, Q. | *Kleinschmidt* .. | 36 | 72 | 134030 (parent) |
| *S. gracilius* .. | Clapham Junction, Brisbane, Q. | *Henderson* 301 | 12 | 24 | 073152 |
| | seed ex Clapham Junction, Q. | *Henderson* 128 | 12 | 24 | 121384 |
| | seed ex Dunedin, N.Z. .. | *Baylis* .. .. | 12 | 24 | 081335 |
| *S. nitidibaccatum* | 8 km from Stanthorpe, Q. | *Henderson & Parham* 1241 | 12 | | 140046 |
| | seed ex Applethorpe, Q. .. | *Johnson* .. | 12 | 24 | 081224 |
| | seed ex Moscow, U.S.S.R. | *Vilar Instit.* 1967 seed list 411 | 12 | 24 | 140033 |
| *S. villosum* .. | seed ex Walsh R., Q. .. | *Cunningham* .. | 24 | 48 | 076630 |
| | seed ex Strathalbyn, S.A. .. | *Symon* .. .. | 24 | 48 | 140045 |
| | seed ex Moscow, U.S.S.R. | *Vilar Instit.* 1967 seed list 408 | 24 | 48 | 140044 |
| *S. douglasii* .. | seed ex Moscow, U.S.S.R. | *Vilar Instit.* 1967 seed list 398 | 12 | 24 | 140034 |
| *S. retroflexum* .. | seed ex Eyre Peninsula, S.A. | *Alcock* .. .. | 24 | 48 | 140042 |
| *S. scabrum* .. | seed ex Sunshine nursery, N.S.W., from U.S.A. Exact origin unknown | .. | 36 | | 009749 |

## NATURAL BREEDING SYSTEM AND HYBRIDISM

The breeding system of New Zealand plants of *S. nodiflorum, S. nigrum* and *S. gracilius* was discussed by Baylis (1958), that of European plants of *S. nigrum, S. alatum* and *S. luteum* by Wessely (1960) and Indian plants classified as *S. nigrum* sens. lat. by Venkateswarlu and Rao (1972). These authors generally agree that plants are principally self-pollinating though out-breeding and to a less extent cross-breeding can and probably does occur.

With Australian plants studied in the field and grown under glasshouse conditions, morphology of floral parts and the sequence of floral attitude from the bud stage till dropping, together with the results of some simple bagging tests indicate that the majority are also self-pollinating usually by pollen from the same flower or possibly from other flowers on the same plant. Individual buds and whole inflorescences of *S. nigrum, S. nodiflorum, S. opacum* and *S. villosum* when covered with clear plastic bags invariably set fruit. It seems unlikely that seed is produced apomictically in these species since emasculated flowers bagged to prevent pollination invariably failed to set fruit.

However, in species with larger flowers, e.g. *S. douglasii* and *S. gracilius,* anther dehiscence occurs some short time after the bud opens, by which time the stigma is well clear of the anther pores and remains that way. Cross-pollination and cross-fertilization with pollen from flowers of the same plant or possibly of different plants of the population probably occurs in the majority of flowers. No flowers of *S. gracilius* were bagged but plants grown in a glasshouse set quite large numbers of well developed, well filled fruits without artificial pollination. Plants of *S. douglasii* grown from seed from U.S.S.R. and plants of *S. amethystinum* (Kuntze) Heiser, a related large-flowered species from Central America, grown from seed from U.S.A., set few or no fruit in the glasshouse. Artificial cross-pollination between flowers of the same plant failed to increase the number set but when cross-pollinated with pollen from different plants, a little more fruit was set. Further work with plants from different sources may establish that there is a preferential out-breeding system in these species.

In all species studied the flowers are initially held inverted in which position self-pollination merely by gravity could occur irrespective of the position of the stigma.

Some cross-pollination of usually selfing lines probably occurs to some extent as pollen gathering honey-bees have been observed visiting, without preference, flowers of two diploid taxa growing naturally in close proximity in the field. In addition, anemophilous cross-pollination of sympatric species could easily occur since the smooth-walled pollen is usually dry after dehiscence and is produced in considerable quantities.

Putative hybrids between the two subspecies of *S. nodiflorum* and between *S. nodiflorum* subsp. *nutans* and *S. gracilius* have been found in the field. No such hybrids have been found between taxa of different ploidy levels in the field though under glasshouse conditions spontaneous hybrids between hexaploid *S. scabrum* and diploid *S. nodiflorum* subsp. *nodiflorum* were found on one occasion. A number of apparent hybrids including ones between taxa of different ploidy levels have been noted within herbarium material studied. This was

particularly noticeable in specimens originating in Botanic Gardens, market gardens or trial plots where seed of a number of allied species of *Solanum* has been introduced, intentionally or not, from other areas of the continent or from abroad, and grown in close proximity to one another. Such a situation was observed in trial plots used during the present study. As stated previously, gross reduction of pollen viability, the presence of a large percentage of collapsed grains or a large size range of viable pollen and the presence of intermediate morphological characters have been taken as indications of hybridism between taxa.

## ECOLOGY AND ECONOMICS

Members of the "*S. nigrum* species complex" occur widely in various habitats throughout the world. In Australia most of the species are introduced and persist mainly in disturbed habitats such as garbage tips, near farm and domestic water outlets, in shaded areas round buildings and large spreading trees, on areas of cultivated land, roadways, rain-forest margins and landward slopes of coastal dunes. Wide tolerance of habitat types, ability to flower while still quite young and prolific production of seed no doubt contribute to the persistent weedy nature of the species in this group.

Plants of this group have consistently been suspected of poisoning stock in many parts of the world including Australia (e.g. Bailey, 1881; Cheel, 1917; McBarron, 1955; Everist, 1973). Everist noted that steroidal alkaloids (glyco-alkaloids including solanine, solasonine and solmargine) have been recorded in all species so far tested (5) and recommended that further chemical work would be worthwhile in the light of modern taxonomic findings.

Though all vegetative parts and immature fruits are considered capable of poisoning stock, at times plants can be grazed without ill effect. Some herbarium specimens show signs of cropping and others are accompanied by notes to this effect.

In a feeding test in North Queensland, according to the voucher specimen (BRI), 15 lb (6·8 kg) of plant material of *S. nodiflorum* subsp. *nutans* was fed over 4 days to a young bovine (heifer) without ill effect.

The ripe berries are often said to be eaten with impunity. Personal experience is that the ripe fruit of *S. nigrum, S. nodiflorum* and *S. opacum* can safely be eaten. Acceptable quality jams and conserves have been made from the berries of some species. *S. scabrum* has been cultivated under various names for human consumption as garden huckleberry. Heiser's essay on "the Wonder-berry" (Heiser, 1969) is an interesting and entertaining account of some historical

commercial aspects of this subject. Fruits of *S. scabrum* because of their high concentration of anthocyanin pigments (Francis & Harbone, 1966) have been used as a colorant for apple sauce and fruit juices.

*S. nigrum* is recorded as an ancient famine plant of the Chinese (Baranov, 1967) and Bailey (1883) stated that the herbage of both forms of *S. nigrum* in Queensland (now known to be *S. nodiflorum* and *S. opacum*) may be used as a substitute for spinach.

Plants of *S. nigrum* and *S. nodiflorum* persisting as weeds of cultivation are known to be alternative hosts for insects which attack such crops as Tobacco (*Nicotiana tabacum*), for plant viruses transmitted by insects and for pathogenic bacteria capable of attacking commercial strains of ginger (*Zingiber officinalis*) (Pegg & Moffett, 1971).

## EXPERIMENTAL HYBRIDIZATIONS

The ease with which hybrids can be obtained and the relative fertility of these artificially produced hybrids have been used in taxonomic studies in *Solanum* sect. *Solanum* to define taxa more precisely and determine relationships between them (e.g. Ellison, 1936; Paddock, 1941; Stebbins & Paddock, 1949; Baylis, 1958; Heiser, 1963; Soria & Heiser, 1965; Heiser, Soria & Burton, 1965; Gray, 1968).

In the present studies hybridization of some Australian plants has been used mainly for confirmation of conclusions from morphological observations and to determine the extent of genetic barriers between these and overseas plants. In all cases crosses were reciprocal, each plant being used as pollen and ovulate parent.

These hybrids are discussed more fully where necessary, under the species concerned, but general conclusions may be summarized as follows:—

(*a*) Crosses between *S. nodiflorum* subsp. *nodiflorum* and subsp. *nutans* were readily obtained. In several replicates, F1 plants (18–25% pollen fertile) were selfed or back-crossed to each parent. Randon F2 plants grown to maturity were 0–99% pollen fertile. (Table 3).

(*b*) *S. nodiflorum* subsp. *nutans* when crossed with *S. opacum* failed to set viable seed.

(*c*) *S. nigrum* from Queensland when crossed with *S. nigrum* from New Zealand produced fully fertile F1 progeny.

(*d*) *S. villosum* from Queensland and progeny of seed of the same species from U.S.S.R. (received as *S. luteum*) were morphologically distinct but produced fully fertile F1 progeny.

(*e*) *S. gracilius* from New Zealand when crossed with *S. douglasii* from U.S.S.R. produced F1 progeny with pollen fertility 16–18%. The characteristic foetid odour of the *S. douglasii* parent was noticeably diluted in F1 individuals.

Voucher specimens for parent plants, F1 plants and F2 plants studied in the glasshouse are held in the Queensland Herbarium.

## TAXONOMY

**Solanum** L. Gen. Pl. ed. 5, 85 (1754), subgenus **Solanum,** section **Solanum.** Type species—*S. nigrum* L.

*Solanum* section *Pachystemon* Dun. subsection *Morella* Dun. ** *Morellae Verae* Dun. DC. Prod. 13, 1:28 (1852) *nom. illeg.*

### KEY TO SPECIES OF SOLANUM SECT. SOLANUM IN AUSTRALIA

1. Leaves pinnatisect or bi-pinnatisect, plant prostrate or decumbent; flowers 1 to 3, borne on short lateral leafy shoots; mature fruit green or yellowish, 1–1·5 cm diameter, sclerotic granules many (ca. 10–35), each > 0·8 mm across. Not common: Q, N, V, S . . . . . . . . . . *S. triflorum*

   Leaves entire, sinuate-lobed to somewhat pinnatifid, plant erect, ascending, sprawling (or prostrate in *S. opacum*); flowers (2–)3 to 12 in leafless extra-axillary inflorescences; mature fruit where green or yellowish, < 1 cm diameter with sclerotic granules absent or never more than 4 . . . . . . . . . . 2

2. Plant conspicuously pubescent to tomentose or villous (except occasionally on the upper surface of older leaves and older stems), hairs spreading or antrorsely curved . . 3

   Plant glabrous, sub-glabrous or sparsely pilose (usually more dense on stem apices, young leaves and inflorescences), hairs antrorsely (usually strongly) curved . . 8

3. Corolla lobes triangular to broadly triangular, about as long as or a little shorter than the tube; hairs of the pubescence of differing lengths intermixed, mostly spreading, a varying number or all with a globular glandular tip; mature fruit translucent, yellow, orange, red or shining bright green to brown . . . . . . . . . . 4

   Corolla lobes narrowly oblong to narrowly ovate, longer than the tube; hairs of the pubescence usually uniformly short, mostly ± strongly curved or appearing somewhat appressed (rarely spreading), usually without a gland at the tip; mature fruit opaque, black, purplish black or dull green . . . . . . . . . . 5

4. Mature fruit ellipsoid, longer than broad, yellow, orange or red, without sclerotic granules in the pulp; fruiting calyx herbaceous, not disproportionately enlarged, the lobes spreading or strongly reflexed; mean of pollen size range > 27 $\mu$; plant erect, annual or short lived perennial. Rare: S, nQ . . . . . . . . . . *S. villosum*

Mature fruit spherical or spheroid (where shorter than broad) olive green or light brownish when very ripe, the surface shiny, one pair of sclerotic granules 0·5–0·8 mm across at the apex (below stylar scar); fruiting calyx exceedingly enlarged, membranous, embracing about half the fruit, the lobes ± spreading; mean of pollen size range < 27 μ; plant spreading, strictly annual. Uncommon: Q, N, V, S .......... *S. nitidibaccatum*

5. Anthers at anthesis >2 (rarely only 1·8 or less when petals linear) mm long; calyx lobes appressed to the fruit or somewhat spreading (rarely recurved); mature fruit black, the surface matt .......... 6

Anthers at anthesis < 1·8 (occasionally up to 2) mm long, calyx lobes appressed to the fruit or strongly reflexed; mature fruit black or green, the surface shiny or matt .......... 13

6. Flowers usually > 1·1 cm diameter; style protruding by at least 1 mm beyond the ring of anthers; plant erect or sprawling .......... 7

Flowers usually < 1·2 cm diameter; style level with the top of the ring of anthers or protruding by up to 1 mm; plant erect; infructescence racemiform, peduncle ascending, pedicels decurved or deflexed, alternate on a horizontal rhachis, internodes usually conspicuous; fruit without sclerotic granules; anthers < 3 mm long, mean of pollen size range > 27 μ. Uncommon: S .......... *S. nigrum* subsp. *schultesii*

7. Inflorescence racemiform with at least 2 internodes distinct; flower buds broadly elliptic in outline; sclerotic granules present in the fruit .......... 12

Inflorescence (sub-)umbelliform; flower buds distinctly elongate in outline, petal lobes distinctly elongate; fruiting peduncle horizontally spreading or sharply deflected from near its base; fruit (usually) without sclerotic granules; anthers > 2·3 mm long, mean of pollen size range < 27 μ. Widespread but not common: Q,N,V .......... *S. grácilius*

8. Lobes of the corolla deltoid to broadly triangular about as long as or a little shorter than the tube; mature fruit translucent, orange, or shining green, spherical or ellipsoid (where longer than broad) .......... 4

Lobes of the corolla narrowly oblong to narrowly ovate to semi-elliptic (rarely linear), acute, longer than the tube, mature fruit opaque, black or dull green, spherical or spheroidal (where broader than long) .......... 9

9. Anthers at anthesis ≧ 2 (rarely only 1·8, or even less where petals linear) mm long; mature fruit black .......... 10

Anthers at anthesis ≦ 1·8 (occasionally up to 2) mm long, petals never linear, mean of pollen size range < 27 μ, mature fruit black or green .......... 13

10. Style with stigma from within the ring of anthers to protruding by up to 1 mm; flowers usually < 1·2 cm diameter; plant erect; surface of mature fruit dull or shiny .. 11

Style protruding beyond the ring of anthers by at least 1·5 mm; flowers > 1·2 cm diameter; plant erect or sprawling; surface of mature fruit dull .......... 12

11. Infructescences racemiform, internodes usually conspicuous; peduncle erect or ascending, pedicels deflexed or descending; fruit $< 1 \cdot 2$ cm diameter, the surface matt; calyx appressed to the berry or spreading-recurved; anthers (1·8–) 2–2·5 mm long. Common: all States ................................ *S. nigrum* subsp. *nigrum*

Infructescences (sub-)umbelliform; peduncles horizontally spreading, pedicels divaricate, erect to deflexed in the one cluster; fruit usually $\gg 1 \cdot 2$ cm diameter, the surface highly shiny; calyx strongly reflexed behind the berry; anthers 2·5–3 mm long. Not known naturalized in Australia ........................ *S. scabrum*

12. Plant sprawling; fruiting peduncles bifurcate, deflexed from the base at maturity; mature fruit with numerous (up to 12) sclerotic granules 0·5–1·2 mm across in the pulp; stem tips with young leaves not emitting a foetid odour when crushed; mean of pollen size range $> 28\ \mu$. Rare: V, T .......................... *S. furcatum*

Plant erect or ascending, bushy; fruiting peduncles unbranched, erect or ascending at maturity; mature fruit with few sclerotic granules in the pulp (usually $< 7$), $< 0 \cdot 5$ mm across (rarely absent); stem tips with young leaves emitting a decidedly foetid odour when crushed; mean of pollen size range $< 27\ \mu$. Not known naturalized in Australia ...................................... *S. douglasii*

13. Plant erect, ascending or sprawling, often becoming bushy; peduncle of infructescence erect or ascending, pedicels (2–)4–12; mature fruit black, pulp not decidedly aromatic, sclerotic granules where present $< 0 \cdot 6$ mm across ................ 14

Plant usually prostrate or decumbent, herbaceous; infructescence umbelliform, peduncle from horizontally spreading to strongly deflected from the base, pedicels 2–4(–6); mature fruit green (very rarely black), the pulp sweetly aromatic, sclerotic granules 2 (rarely 4) beneath the stylar scar only, 0·6–1·2 mm across; calyx lobes appressed to the berry. Common: Q, N, V, T .............................. *S. opacum*

14. Plant widespreading or at length sprawling; mature leaves distinctly discolorous, margins regularly toothed; infructescence sub-racemiform, at least one internode conspicuous, pedicels deflexed or decurved; surface of mature fruit dull matt black; seed $> 1 \cdot 5$ mm long usually $< 40$ per berry; mean of pollen size range $> 23\ \mu$. Rare: sS ....................................................... *S. retroflexum*

Plant widespreading, ascending to erect; mature leaves not distinctly discolorous, margins entire, sinuate or regularly few-toothed; infructescence umbelliform (or sub-umbelliform), pedicels decurved or divaricate; surface of mature fruit with a high shine, purplish-black; seed $< 1 \cdot 6$ mm long usually $> 40$ per berry; mean of pollen size range $< 23\ \mu$ .................................. *S. nodiflorum*

Adult leaves entire or sinuate; infructescences with (4–)6–9(–12) fruits, the pedicels divaricately spreading; fruit without sclerotic granules in the pulp. Restricted: seQ ...................................... subsp. *nodiflorum*

Adult leaves dentate, sinuate or rarely entire; infructescences with (2–)4–6(–8) fruits, the pedicels all decurved, fruit with (1–)4–6(–8) sclerotic granules in the pulp. Common: Q, N, V. Uncommon: Y, W .......... subsp. *nutans*

The descriptions of pubescence in this key ignore the small stipitate multicellular glands that are present in varying densities on all plants considered in this study.

With respect to generalized distributions, Q = Queensland, N = New South Wales, V = Victoria, T = Tasmania, S = South Australia, W = Western Australia, Y = Northern Territory and lower case letters refer to compass direction (e.g. n = north).

**Solanum nigrum** L. Sp. Pl. ed. 1:186 (1753); Benth. Fl. Aust. 4:446 (1869); F. Muell. Fragm. 6:145 (1868); Domin, Biblioth. Bot. 89:572 (1928); Moore & Betche, Hbk Fl. N.S.W., 332 (1893); Curtis, Stud. Fl. Tas. 3:505 (1967); Beadle *et al.* Fl. Sydney Region 488 (1972); Willis, Hbk Pl. Vict. 2:551 (1972). Type: ⊖ [sign for central Asia], hb. Linnaeus [no. 248.18] (lectotype LINN, not seen; IDC 177–5.138: III.4 (248.18)).

MISAPPLIED NAME:

*Solanum opacum* auct. non A.Br. & Bouché; Cheel, Proc. Linn. Soc. N.S.W. 42:595 & pl. 30 (1917).

Annual or short lived perennial and then somewhat shrubby, erect or ascending, up to 1 m tall, often sprawling or sometimes compact and only 3 cm high. Stems green or variously marked with purple, round angular or narrowly winged by the decurrent leaves, ridges smooth, glabrous, sub-glabrous or rarely pilose with numerous strongly curved or spreading eglandular or also glandular hairs especially between the ridges or wings. Leaves deep green or variously tinged with purple; blades ovate to elliptic, acute, obtuse or somewhat acuminate with the tip obtuse, contracted or gradually (often long) attenuate to the petiole, up to 13 cm long and 7·5 cm broad though usually much smaller, entire, sinuately lobed or crenate, with few to many strongly curved or occasionally spreading, eglandular or rarely glandular hairs on both surfaces, more numerous along the veins and towards the margins; petioles 1–5(–7) cm long, ± narrowly winged. Inflorescences (3–)5–12-flowered; peduncle simple or rarely forked, erect or ascending, 0·8–2·5 cm long in flower, up to about 3·5(–5) cm in fruit; rhachis spreading or decurved, internodes usually conspicuous; pedicels decurved to ascending in flower, pendulous or decurved in fruit, 0·6–1 cm long. Flowers 6–12(–18) mm diam. Calyx in flower, campanulate, 1·5–1·8(–2·2) mm long, in fruit flattened, ± spreading or rarely somewhat recurved, up to ± 8 mm diam.; lobes semi-elliptic to ± triangular, obtuse, 0·3–0·8(–1·2) mm long and 0·2–0·8(–1·3) mm broad in flower, enlarging to about 2·0(–4·0) mm long and 2(–2·5) mm wide in fruit, sparsely pubescent outside especially towards the tip, hairs strongly curved. Corolla stellate, white or rarely tinged with purple especially on the outer surface (very rarely ± purple striped); lobes ovate (rarely linear), acute, 2·2–4(–5·8) mm long and up to 2·5(–3·5) mm broad, puberulous outside towards the tip and upper margins. Stamens 2·5–4·5 mm long; filaments spreading hairy on the inner side; anthers (1·8–)2–2·7 mm long; pollen (25–)27–33(–35) μ across. Style straight, spreading hairy in the lower $^{2}/_{3}$, 3·5–4 mm long; stigma 0·4 mm across, level with the tips of the anthers or protruding by up to 1 mm. Mature fruit globose or slightly depressed, purplish black to jet black, opaque, dull or somewhat shining, 7–9·5(–10) mm long and 8–9·5(–11·5) mm wide, without sclerotic granules (or very rarely 1 or 2

granules less than 0·6 mm across); seeds 15–45, 1·8–2·2 mm long and 1·2–1·6 mm wide. Chromosome number: 2n(6x) = 72. Infructescence—Plates 6 (F) and 7 (G) and (K).

The species is represented in Australia by two subspecies, both introduced. Subspecies *schultesii* is distinguished from subspecies *nigrum* principally by its denser indumentum of spreading, mostly gland-tipped hairs (see also Wessely, 1960).

### (a) **Solanum nigrum** subsp. **nigrum**

QUEENSLAND.—BURKE DISTRICT: Hughenden, Jul 1963, *Everist* 7291 (BRI); Flinders R. crossing, 40 miles SW of Normanton, May 1967, *Symon* 4954 (BRI, ADW). COOK DISTRICT: Emerald Ck. irrigation channel, Mareeba, Jul 1963, *Cunningham* (BRI); ca 15 miles SW of Mareeba, Oct 1967, *Cunningham* (BRI). NORTH KENNEDY DISTRICT: Charters Towers, *Plant* NSW 71986 (NSW); Burdekin R., 30 miles from Ayr, *Michael* 1689 (BRI); Range View, ca 30 miles SE of Ravenswood, Jun 1952, *Everist* 5178 (BRI); Bowen Delta [20° 00′ S., 148° 15′ E.], Jul 1971, *Wright* 19 (BRI). PORT CURTIS DISTRICT: Calcap Dam, 8 miles E of Biloela, Nov 1967, *McDonald* 373 (BRI); Dart's Ck., near Ambrose, ca 5 miles N of Mt. Larcom, Nov 1963, *Darvall* (BRI). MORETON DISTRICT: Nambour, Dec 1957, *Burchill* (BRI); Kentville, ca 11 miles ENE of Gatton, Oct 1965, *Henderson* 123 (BRI); Mt. Mee, ca 13 miles W of Caboolture, Jun 1968, *Henderson* 404 (BRI); 2 miles E of Kilcoy, Oct 1968, *Springall* (BRI). DARLING DOWNS DISTRICT: "Rockwood", ca 20 miles SW of Chinchilla, Nov 1969, *Pedley* 3012 (BRI); Stanthorpe, Feb 1964, *Baker* (BRI); 28° 35′ S., 151° 58′ E., The Summit, ca 8km NNE of Stanthorpe, Feb 1972, *Henderson & Parham* 1242 (BRI). MARANOA DISTRICT: near Roma, Mar 1970, *Petrie* (BRI). MITCHELL DISTRICT: bed of Thompson R., Jundah, Nov 1970, per *Hall* (BRI).

NEW SOUTH WALES.—NORTH COAST: Singleton, May 1936, *anon.* NSW 72006 (NSW); Lismore, Sep 1949, *Fiford* NSW 72005 (NSW); Grafton, May 1953, *O'Grady* NSW 71905 (NSW); near Kyogle, Mar 1969, *Wright* (BRI). CENTRAL COAST: Penhurst, May 1911, *Cheel* NSW 72038 (NSW); Emu Plains, Feb 1915, *Chapman* NSW 72040 (NSW); Government Domain, Sydney, Mar 1916, *Cheel* NSW 72027 (NSW); Woy Woy, Oct 1916, *Cheel* NSW 71914 (NSW); Sydney Botanic Gardens, Nov 1921, *Cheel* NSW 99973 (NSW); Ashfield, Mar 1923, Feb 1926, Nov 1932, *Cheel* NSW 72012, NSW 99820, NSW 71941 (NSW); Glenfield, May 1923, *Leddon* NSW 72014 (NSW); Sydney University Grounds, Sydney, Oct 1930, *Harris* (CANB); Windang I., Lake Illawarra, Apr 1938, *Rodway* [NSW 71890] (NSW); Richmond, Apr 1948, *Musson* NSW 71995 (NSW); Cheltenham, Mar 1949, *Johnson* NSW 71921 (NSW); Victoria Park, University of Sydney, Nov 1952, *Evans* NSW 72024 (NSW); Mrs. Macquaries Pt., Sydney, Aug 1955, *Baylis* S54A (NSW, MEL); The Lake, Scarborough Park, Kogarah, Jan 1965, *Constable* 5632 (NSW); Epping, Sydney, Feb 1966, *Ingram* (ADW). SOUTH COAST: Nowra, Feb 1952, Mar 1952, *Rodway* [NSW 100859, NSW 100858] (NSW). CENTRAL TABLELANDS: Hilltop, Jan 1915, Jan 1916, Apr 1916, *Cheel* NSW 67714, NSW 71937, NSW 72031 (NSW), May 1916, *Cheel* (BRI); Medlow, Blue Mts., Mar 1916, May 1916, *Griffiths* NSW 72009, NSW 72029 (NSW); Abercrombie Caves, Mar 1955, *Constable* NSW 31331 (NSW). SOUTHERN TABLELANDS: Canberra, May 1918, *Cambage* NSW 72010 (NSW); Turner, Canberra, Feb 1957, *Pullen* 44 (CANB); Hall, Feb 1960, *D'Arnay* 111 (CANB); N slope of Black Mt., Canberra, Feb 1962, *McKee* 8944 (NSW, CANB); Lake George, Apr 1963, *Burbidge* 7391 (MEL, CANB, BRI). NORTH WESTERN SLOPES: Gunnedah, May 1926, *Cheel* NSW 72007 (NSW); Mt. Exmouth, Warrumbungle, S of Coonamble, Apr 1952, *Johnson & Constable* NSW 20565 (NSW). CENTRAL WESTERN SLOPES: Dubbo, Nov 1887, *Betche* NSW 72035 (NSW); Ardlethan, Oct 1916, *Cambage*

NSW 71998 (NSW); Young, Dec 1920, *Grafton* 11 (NSW). SOUTH WESTERN SLOPES: Albury, Mar 1909, *Albury Brewing Co.* NSW 71999 (NSW); Kangiara Mines near Bowning, Apr 1917, *Cock* NSW 72030 (NSW); Cootamundra, May 1939, *anon.* NSW 72015 (NSW). WESTERN PLAINS: Louth, Sep 1910, *Abrahams* 315 (NSW); Yanco, Nov 1913, *Breakwell* NSW 72003 (NSW); Wooloondool, 7 miles from Hay, Feb 1916, *Froggatt* NSW 71939 (NSW); Cowra Experiment Farm, Feb 1920, *Henry* NSW 72008 (NSW); Boree Plains, Oaklands, Mar 1920, *Holland* (NSW); Jerilderie, Mar 1924, *Hildred* NSW 72011 (NSW); Cumalong Camp near Mathoura, Jan 1958, *McGillivray* 683 (NSW); Yanco Ag. Research Station near Leeton, Nov 1965, *Swain* (NSW); about 25 miles SE of Louth, Apr 1967, Jul 1968, *Moore* 4840, 5257 (CANB); Griffith, Dec 1970, *Watt* (BRI). FAR WESTERN PLAINS: near Darling R., Victorian Expedition, in 1860, *Beckler* (MEL); Broken Hill, May 1917, *Cleland* NSW 72017 (NSW), Sep 1918, *Andrews* NSW 72016 (NSW), May 1920, *Morris* 202 (NSW), Mar 1924, *Johnston* NSW 67709 (NSW), Apr 1930, *Morris* (BRI); Kudgee Lake, 55 miles SE of Broken Hill, Jul 1955, *Constable* NSW 35630 (NSW); Lake Cawndilla near Menindee, Jul 1955, *Constable* NSW 37874 (NSW); Mt. Mulyah, about 50 miles NW of Louth, Dec 1966, *Moore* 4719 (CANB); Tapio Stn., 6 miles N of Buronga near Wentworth, Apr 1968, *Henshall* NSW 99961 (NSW). CULTIVATED: Ashfield (seed ex Botanic Gardens, Madrid, Spain), Jan 1916, *Cheel* NSW 72026 (NSW).

VICTORIA.—GIPPSLAND DISTRICT: East Gippsland, *Beauglehole* 37803 (ADW); 3 miles S of Leongatha (1½ miles N of Koonwarra), Apr 1964, *Aston* 1180 (MEL). NORTH EAST DISTRICT: 3 miles W of Dandongadale, Feb 1961, *Muir* 2058 (MEL). CENTRAL DISTRICT: Western Port, in 1891, *anon.* (MEL); Braybrook, Apr 1899, *St. John* (MEL); Eltham, Feb 1904, *St. John* (MEL); Botanic Gardens, Melbourne, Mar 1919, *Baker* (MEL); Brighton, Feb 1963, *Willis* (MEL); McCrae, Feb 1963, *Willis* (MEL); Rickett's Pt., Port Philip Bay, Mar 1963, *Aston* 937 (MEL); Botanic Gardens, Melbourne, Mar 1963, *Allender* (MEL); North Geelong, Jan 1964, *Muir* 3174 (MEL); Frankston, May 1965, *Everist & Willis* (BRI); Altona, Nov 1967, *Cullimore* 106 (MEL, AD); Domain Gardens, Melbourne, *Weindorfer* 762 (MEL). NORTH CENTRAL DISTRICT: Waaia, Mar 1959, *Cleaves* (MEL); Mt. Bolton, between Learmouth and Lexton, Mar 1964, *Willis* (MEL). NORTHERN DISTRICT: St. Arnaud, in 1889, *Gorrie* (MEL); Echuca, in 1889, *King* (MEL); Moorilum, in 1890, *Martin* (MEL); Lockwood, *Bissil* 14 (MEL). WESTERN DISTRICT: Hawkesdale, Dec 1899, *Williamson* (MEL), Jan 1902, *Williamson* NSW 71984 (NSW); Viewpoint Rock, Grampians, Nov 1959, *Symon* 222 (ADW); Mt. Napier, ca 10 miles SSE of Hamilton, May 1963, *Willis* (MEL); Mumbannar, Dec 1967, *Lewis* (ADW); Dundas Range, Grampians, Jun 1968, *Beauglehole* 25280 (ADW); Mt. Sturgeon, Grampians, Jun 1968, *Beauglehole* 25297A (ADW). MALLEE DISTRICT: Mildura, Mar 1916, *Cleland* [NSW 72013] (NSW); Red Cliffs, Aug 1955, *Baylis* S54C (MEL, NSW); 2 miles NE of Red Cliffs, Feb 1967, *Cullimore* 40 (MEL, AD). UNPLACED: Inland Victoria, in 1878, in 1886, *anon.* (MEL). CULTIVATED: Dunedin, N.Z. (seed ex Lake Hattah, NW Victoria), *Baylis* S54B (MEL). ABNORMAL FORM WITH NARROW PETALS: ca 3·5 miles SE of Pomonal, Apr 1968, *Beauglehole* 25068 (ADW).

TASMANIA.—King Is., *Mueller* (MEL); "Kelvedon" near Swansea, *Story* (MEL); South Arm, Feb 1899, *Rodway* [NSW 71897] (NSW); Woodcutter's Point, Jan 1901, *Rodway* [NSW 71966] (NSW).

NORTHERN TERRITORY.—DARWIN & GULF DISTRICT: near Adelaide R., in 1890, *anon.* 1146 (MEL); Port Darwin, Jan–Jun 1891, *Holtze* 80 (GFW). BARKLY TABLELAND DISTRICT: Plenty R. crossing, 94 miles W of Tarlton Downs Homestead, Apr 1967, *Maconochie* 114 (AD). ALICE SPRINGS DISTRICT: Todd R., 6 miles N of Alice Springs, Nov 1954, *Chippendale* (BRI, NSW, CANB), *Winkworth* 713 (CANB); 13 miles SE of Alice Springs, Aug 1962, *Nelson* 523 (BRI, MEL, AD, CANB); 23° 47′ S., 133° 40′ E., 4 miles S of Simpson's Gap,

Feb 1967, *Byrnes* 169 (ADW); Trucking yards, Alice Springs, Jun 1967, *Nelson* 1499 (ADW); Undoolya Gap bore, 17 miles E of Alice Springs, Dec 1968, *Nelson* 1795 (AD); Stud Bore, Todd River Stn., Sep 1969, *Nelson* 1959 (ADW).

SOUTH AUSTRALIA.—SOUTH EAST: Penola, *Mueller* (MEL); Lake George near Beachport, Nov 1959, *Wilson* 1135 (AD); 11 km W of Penola, Nov 1959, *Wilson* 1282 (AD, ADW); 20 miles NW of Keppok, Mar 1960, *Goldfinch* (ADW); Shores of Brown Lake, Mt. Gambier, Mar 1961, *Symon* 1181 (ADW, PERTH); ca 10 km W of Naracoorte, Sep 1961, *Hunt* 110 (AD); Piccaninnie Blue Lake, ca 20 km E of Port MacDonnell, Aug 1964, *Lothian* 2937 (AD); Mt. Gambier, Aug 1967, *Southcott* B377 (AD), Mar 1968, *Simpson* (ADW); near Tantanoola, ca 32 km NW of Mt. Gambier, Apr 1967, *Wilson* 743 (AD). MURRAY MALLEE: Tailem Bend, ca 110 km SE of Adelaide, Jan 1937, *Ising* (AD); Cooke Plains, ca 40 km SE of Murray Bridge, Oct 1959, *Sharrad* 288 (AD); Harrison's Ck., ca 3 km S of Palmer (ca 21 km NW of Mannum), Mar 1961, *Donner* 26 (AD); Murray Mallee Plains, ca 13 km SE of Cambrai, Mar 1964, *Jackson* 583 (AD); Murray R., ca 67 km E of Adelaide, Mar 1965, *Donner* 1292 (AD); upper Murray R. between Waikerie and Barmera, Nov 1965, *Eichler* 18367 (AD); Renmark, Aug 1967, *Stoeckel* W9 (ADW); Wellington, mouth of Murray R., Mar 1968, *Weber* 668 (AD); Warkerie, E of Morgan, *Tough* (ADW). LAKE FROME BASIN: Bumbumbie Springs, Koonamore, Sep 1928, *Paltridge* (CANB); 15 miles NE of Mundy Crk. on road to Murnpeowie Stn., Aug 1968, *Symon* 5599 (ADW); Moolawatana Stn., NE South Aust., Aug 1968, *Symon* 5945 (ADW); Koonamore Stn., ca 400 km NNE of Adelaide, May 1971, *Crisp* 121 (AD). KANGAROO ISLAND: Distress [D'Estrees?] Bay, Jan 1923, *Ising* (AD); Kingscote, Sep 1963, *Jackson* 281 (AD); Stokes Bay, Apr 1968, *Davison* (ADW). MOUNT LOFTY RANGES: Kooringa near Burra, upper Mt. Lofty Ranges, Mar 1895, *Brummitt* (AD); Waterfall Gully, ca 10 km SE of Adelaide, Apr 1921, *Cleland* (AD), Oct 1961, *Donner* 400 (AD); Encounter Bay, 75 km S of Adelaide, Aug 1924, Jan 1925, Feb 1925, *Cleland* (AD); Kinchina, ca 60 km SE of Adelaide, Apr 1924, Jun 1925, *Cleland* (AD); Victor Harbour, Sep 1924, *Adcock* (AD), Aug 1969, *Johnsson* 44 (AD); Angaston, 65 km NW of Adelaide, Feb 1925, *Cleland* (AD); Mt. Lofty Range National Park, Mar 1933, *Cleland* (AD); Strathalbyn, ca 45 km SE of Adelaide, Mar 1948, *Hender* (AD); Stirling, ca 15 km SE of Adelaide, Apr 1957, *Booth* 77 (AD), Feb 1960, *Ising* (AD); Shores of Millbrook Reservoir, Mar 1958, *Symon* (ADW); Wright I., Victor Harbour, ca 75 km S of Adelaide, Jan 1960, *Lothian* 189 (AD); Maralinga, ca 15 km SE of Adelaide, Aug 1960, *Turner* (AD); Morialta, Feb 1961, *Symon* 1165 (ADW); Mt. Bold, ca 25 km SE of Adelaide, Jun 1963, *Fagg* (AD); Goolwa, Jul 1966, *Lewis* (ADW); Mt. Lofty Botanic Gardens, ca 15 km SE of Adelaide, Apr 1967, *Weber* 544 (AD); Summertown, Oct 1967, *Baghurst* (ADW); ca 40 miles NE of Adelaide, Oct 1967, *Belcher* 579 (ADW); Coromandel Valley, Oct 1967, *Young* (ADW); Brady Ck., ca 5 km E of Tothill Range (ca 130 km N of Adelaide), Aug 1968, *Krachenbuehl* 2248 (AD); Saunders Ck. Gorge, ca 70 km NNE of Adelaide, Jul 1969, *Blaylock* 1300 (AD); Normanville sand dunes, ca 65 km SW of Adelaide, Sep 1969, *Whibley* 2925 (AD); Torrens Gorge, May 1970, *Spooner* 866 (AD); The Crescent, Crafers, ca 12 km SE of Adelaide, Mar 1972, *Henderson* 1270 (BRI, AD); NW portion Mt. Lofty Botanic Garden, ca 12 km ESE of Adelaide, Mar 1972, *Henderson* 1273 (BRI, AD). ADELAIDE PLAINS: Adelaide, in 1898, *Cleland* [NSW 71968] (NSW); Halletts Cove, ca 25 km SSW of Adelaide, Apr 1924, *Ising* (AD), Jul 1967, *Smith* 13 (AD); Fullarton, Aug 1924, *Cleland* (AD); Outer Harbour, Adelaide, Apr 1926, *Rodway* [NSW 71894] (NSW); Port Noarlunga, Aug 1943, *Perry* (CANB); Adelaide, Oct 1952, *Martin* (AD); Waite Institute, Adelaide, Jul 1955, *Feuerhardt* (ADW); Roseworthy, ca 55 km N of Adelaide, Jul 1962, *Wilson* 2271 (AD); Clapham, Jan 1963, *Symon* (ADW); ca 72 km WNW of Adelaide, Oct 1966, *Blaylock* 261 (AD); Eden Hills, Nov 1966, *R.W.P.* (AD); Unley Park, Adelaide, Jun 1967, *Southcott* B336 (AD), Apr 1968, *Smith* 1088 (AD); Underdale, banks of Torrens River, Aug 1967,

*Lewis* 48 (ADW); Athelstone, Apr 1968, *Ivany* (ADW); Two Wells, ca 40 km N of Adelaide, Jun 1968, *Blaylock* 880 (AD); Hyde Park, Adelaide, Apr 1969, *Southcott* B590 (AD); Hartley Grove, Glen Osmond, Jun 1969, *Symon* (ADW); Highbury, ca 15 km NE of Adelaide, Nov 1970, *Spooner* 1342. YORKE PENINSULA: Lower Mambray Ck., Jun 1960, *Symon* 450 (ADW); 5 km SW of Yorketown, Apr 1961, *Donner* 60 (AD); Yorketown, Mar 1963, *Donner* 725 (AD); Clements Gap, Aug 1964, *Symon* 2918 (ADW); Maitland, Aug 1964, *Symon* 2921 (ADW); ca 11 km from Bute (ca 130 km NNW of Adelaide), Feb 1966, *Copley* 115 (AD); Port Clinton, Feb 1966, *Redgen* (ADW); Wallaroo, ca 140 km NNW of Adelaide, May 1966, *Copley* 253 (AD); ca 5 km E of Ninnes (120 km NW of Adelaide), Jan 1967, *Copley* 1088 (AD); between Kadina and Paskeville, ca 7 km SSE of Kadina, Jul 1970, *Blaylock* 1431 (AD). FLINDERS RANGE: Quorn, Jan 1907, *Maiden* NSW 71983 (NSW); Merna Merna, 22 miles S of Hawker, Apr 1955, *Hilton* 1257 (ADW); Leigh Ck., ca 365 km NNE of Port Augusta, Sep 1961, Sep 1963, *Lothian* 760, 2364, 2350 (AD), Aug 1968, *Symon* (ADW); Wilpena, May 1962, *Symon* 2134 (ADW); Martin's Well, ca 80 km NE of Port Augusta, Sep 1962, *Donner* 534 (AD); Lower Flinders Range, ca 50 km SSE of Port Pirie, Aug 1963, *Gardiner* 23 (AD); ca 8 km E of Nepabunna Stn. (ca 50 km E of Copley), Nov 1964, *Lothian* 3202 (AD); Alligator Gorge, ca 45 km SE of Port Augusta, Dec 1967, *Blaylock* 846 (AD); Wilpena Ck. near Wilpena Pound (ca 50 km NNE of Hawker), Apr 1968, *Orchard* 338 (AD); ca 5 km SE of Termination Hill (ca 64 km S of Maree), Jun 1968, *Orchard* 528 (AD); Paralana Springs, Northern Flinders, Aug 1968, *Symon* 6090 (ADW); Mernmerna, ca 150 km NE of Port Augusta, Oct 1968, *Weber* 698 (AD); Aroona Valley, ca 25 km NW of Oraparinna homestead, Sep 1971, *Jackson* 1698 (AD); Oraparinna National Park, ca 160 km NNE of Port Augusta, Sep 1971, *Weber* 2478 (AD). EYRE PENINSULA: Flinders I., Jan 1924, *Osborn* NSW 71982 (NSW); Chilpuddie Rock, ca 20 km N of Minnipa, Oct 1939, *Ising* (AD); Port Lincoln, Dec 1941, *Cleland* (AD); Buckleboo, ca 40 km WNW of Kimba, Mar 1959, Apr 1959, *Rohrlach* 217, 290 (AD); Fowlers Bay, Sep 1959, *Symon* (ADW); Inila Rock, 14 miles N of Koonibba, Sep 1959, *Symon* (ADW); Cape Donington, ca 10 km E of Port Lincoln, May 1963, *Wilson* 2660 (AD); 2 miles N of Cowell, Feb 1965, *Pearce* (ADW); ca 2 km W of Old Uley homestead, ca 30 km W of Port Lincoln, Aug 1967, *Whibley* 1850 (AD); S of Bascombe Well, Oct 1967, *Alcock* 1531 (AD); ca 11 km SW of Bascombe Well homestead (25 km WSW of Lock), Oct 1967, *Wheeler* 665 (AD); Hundred of Blesing, South Eyre Peninsula, Oct 1967, *Symon* 5486 (ADW, AD); ca 25 km SW of Port Augusta, Aug 1968, *Rix* (AD); Hincks National Park, Oct 1968, *Wheeler* 792 (AD); Pearson I., Jan 1969, Feb 1969, *Symon* 6608, 6635 (ADW); ca 180 km NNW of Port Lincoln, Apr 1969, *Blaylock* 1219 (AD); Hundred of Hill, ca 40 km NE of Kyancutta, Apr 1969, *Blaylock* 1238 (AD). GAWLER RANGES: near Yardea, ca 210 km W of Port Augusta, Jun 1968, *Wilson* 832 (AD). LAKE TORRENS BASIN: Lake Torrens Plateau, ca 3 km N of South Gap, Sep 1968, *Weber* 1217 (AD). LAKE EYRE BASIN: ca 140 km WNW of Maree on road to Strangways, *Cleland* (AD). NULLARBOR PLAINS: Koonalda Cave, near Eyre highway, ca 65 miles E of Eucla, West Aust., Sep 1963, *Willis* (MEL); ca 5 km N of Koonalda homestead, Sep 1960, *Wilson* 1664 (AD), Sep 1965, *Anway* 345 (AD); Sink Hole, Koonalda, Feb 1967, *Symon* 4531 (ADW, NSW). NORTH WEST PLAINS: Yudnapinna, Jan 1940, *Douglas* (ADW); Maralinga, ca 30 km N of Watson, Sep 1960, *Turner* (AD); Wynbring Rocks, Feb 1965, *Symon* 3430 (ADW); Woomera near Pimba, ca 150 km NNW of Port Augusta, May 1964, *Lothian* 2671 (AD). ABNORMAL FORM WITH NARROW PETALS: Torrens Gorge above Castambul, ca 17 km ENE of Adelaide, Jan 1958, *Eichler* 14625 (AD); Leg of Mutton Lake, Mt. Gambier, Oct 1964, transplanted to Waite Research Institute, *Symon* (ADW); Waite Institute grounds, Adelaide, Jan 1965, *Symon* (ADW); Hesso Stn., Sep 1966, *Symon* 4065 (ADW); Highbury, Feb 1969, *Symon* 6690 (ADW).

NOTE.—Specimens of *S. nigrum* may have been collected near Adelaide by Mueller about 1848. See note under *S. opacum* specimens list.

WESTERN AUSTRALIA.—SOUTH WEST PROVINCE: Eyre District—Figure-of-Eight I., Recherche Archipelago, Nov 1959, *Willis* (MEL). Stirling District—Kojonup, Nov 1966, *Howard* (PERTH, ADW). Warren District—Karridale, Dec 1898, *Helms* NSW 71981 (NSW); Snake I., Nornalup Inlet, Dec 1912, *Jackson* NSW 71980 (NSW); Margaret R., Mar 1953, *Pearce* (PERTH). Darling District—Perth, Apr 1898, *McKaye* (PERTH); South Perth, Apr 1923, *Canie* (PERTH), Feb. 1948, *Royce* 2555 (PERTH), Sep 1967, *Wilson* 6199 (PERTH); Fremantle, Apr 1926, *Rodway* [NSW 71896] (NSW); King's Park, Perth, Aug 1934, *Roe* 266 (CANB), Sep 1943, *Bennett* (PERTH); S end of Garden I., Mar 1960, *Aplin* 648 (PERTH); Muchea, Jan 1961, *Mann* F (PERTH); W of Rockingham, Nov 1961, *Aplin* 1231 (PERTH); Bibra Lake, Nov 1961, *George & Marchant* 3172 [B] (PERTH); 40 miles W of Mt. Barker, Dec 1963, *Carpenter* (ADW); Yanchep National Park, Jan 1964, Jul 1964, *James* 165, 232 (PERTH); Waterloo, Aug 1967, *Royce* 8391 (PERTH); Kwinana, Feb 1968, *Flick & Co.* (PERTH). Irwin District—41 miles N of Geraldton, Jul 1967, *Symon* 5449 (ADW, PERTH); Kalbarri National Park ca 30 km NNW of Ajara, May 1968, *Wilson* 6754 (PERTH). EREMEAN PROVINCE: Coolgardie District—Kalgoorlie, Sep 1967, *Scrymgeour* 2128 (PERTH). Austin District—Sandstone, Jul 1967, *Symon* 5462 (ADW, PERTH); 2 miles S of Belele Stn. homestead, NW of Meekatharra, Aug 1969, *Saffrey* 760 (PERTH).

This subspecies commonly occurs in disturbed areas on a variety of soil types throughout the mainland continent and Tasmania with the possible exception of wet tropical and sub-tropical or temperate coastal regions of Queensland where the species appears unable to persist. The degree to which it is able to flourish in even maritime habitats in drier areas of southern and western Australia supports a supposed evolution of the species in regions with a predominantly mediterranean type climate.

The relatively late date of collection of the oldest dated Australian specimen available to me (near Menindee, in 1860, *Beckler* MEL, but see note under *S. opacum*) suggests that the species is alien to Australia though the widespread localities of other early collections (i.e. between 1860 and 1895) together with the present extensive distribution (Fig. 2) indicate that it was probably introduced separately on a number of occasions. That early specimens should be from the far interior of the continent is intriguing. Since the species was used as a vegetable for many centuries by old cultures to the north-west of Australia (Baranov, 1967) introduction by such agents as migratory birds and subsequent unintentional dispersal by aborigines known to relish the fruits of native *Solanum* species including *S. opacum,* could have occurred quite independently of European settlement from 1788 on the eastern coast.

(b) **Solanum nigrum** subsp. **schultesii** (Opiz) Wessely, Fedde. Rep. 63:311 (1960). Based on *S. schultesii.*

*S. schultesii* Opiz in Bercht., ök. fl. Böhm. 3:24–25 no. 479 (1843). Type: hb. Opiz no. 8188 (holotype PR, not seen; isotypes?)

SOUTH AUSTRALIA.—MOUNT LOFTY RANGES: The Crescent, Crafers, ca 12 km SE of Adelaide, Mar 1972, *Henderson* 1271 (BRI, AD), May 1972, *Weber* 3032 (BRI, AD); NW portion Mt. Lofty Botanic Garden, ca 12 km ESE of Adelaide, Mar 1972, *Henderson* 1274

(BRI, AD). CULTIVATED: Botanic Gardens, Brisbane, Nov 1963, *Henderson* s.n. (BRI); Indooroopilly, Brisbane, (seed ex Waite Agric. Res. Institute, *Symon* 1944), Feb 1968, Feb 1973, *Henderson* 352, 1411 (BRI).

This subspecies occurs only in sheltered, moist areas of the Flinders Ranges south-east of Adelaide where it is associated with populations of subsp. *nigrum*.

There appears to be no published account regarding typification of *S. nigrum* L. In the absence of a holotype, specimen 248·18 in the Linnean herbarium is selected as lectotype because

(1) it agrees with the protologue diagnosis
(2) it is labelled "nigrum" in Linnaeus's handwriting
(3) by bearing the abbreviation ⊖ in Linnaeus's handwriting it could well have been in his herbarium prior to 1753
(4) its selection preserves generally accepted current usage of the name in the strict sense.

Baylis (1958) in studying species of *Solanum* sect. *Solanum* applied the name *S. nigrum* L. to a New Zealand hexaploid taxon on the basis of hybridization experiments with plants considered native and others raised from seed from Portugal, and examination including measurement of pollen grain sizes of a specimen in the Linnean herbarium (the lectotype of *S. nigrum*). In addition he considered hexaploid plants he collected from Australia were also of *S. nigrum*.

Examination of Baylis's specimens labelled *S. nigrum* from New Zealand, Victoria and New South Wales (MEL) shows that these are conspecific with a large number of other specimens from Australia. It is clear from the microfiche that the lectotype in the Linnean herbarium supports the application of this binomial to all this Australian material.

Plants grown from New Zealand seed supplied by Prof. Baylis were identical with Australian plants and others grown from seed from the Vilar Institute, Moscow, U.S.S.R. Reciprocal cross-pollinations between New Zealand and Queensland plants produced F1 and F2 progeny which was highly fertile and morphologically typical of the species. Australian material agrees almost exactly with a selection of over 40 very uniform specimens labelled *S. nigrum* L. from localities scattered throughout Europe, lent by the Herbarium des Botanischen Institute, Greifswald (GFW). This material contained specimens examined by Dr. I. Meindke-Wessely including some cited in her paper (1960) and of plants grown by her at Greifswald.

Specimens from Epping, Essex, England (*White* 11250, BRI) are a good match for Australian material. Odashima's figure 2, F (1936) shows probably the extreme to which the calyx lobes can spread, a condition which has not been noted in Australian plants.

Application of the name *S. nigrum* subsp. *schultesii* to the conspicuously spreading glandular hairy South Australian plant with black fruit is based on four specimens (GFW) of plants grown from seed from European localities by Wessely and descriptions in her paper and Opiz's protologue. Though Wessely stated she saw no type material, she reduced Opiz's species to subspecific rank under *S. nigrum* on the basis of a large number of herbarium specimens from Europe and her cultivated plants. Subspecific rank was accorded this taxon on the basis of its "ökologischen Isolierung" from typical *S. nigrum*. Australian plants are not discordant in any way with Opiz's description.

Bentham, Mueller and Domin considered *S. nigrum* in a very broad sense and applied the name to all Australian material of *Solanum* sect. *Solanum*. The material cited by Bentham (MEL) contains specimens of *S. nigrum* and *S. opacum*. Judging by his material (MEL) Mueller's records also referred to these species. After seeing Mueller's specimens and collecting others in Queensland, Domin included specimens of *S. nodiflorum* under *S. nigrum* also though he maintained as variety *pterocaulon*, specimens with angled stems and prickle hairs or pricklets on these angles. Mueller's collection from Murray River, 1853 (MEL) cited by Domin as variety *chlorocarpum* is a specimen of *S. opacum*. Brown's description of *S. nigrum* appears to apply solely to *S. opacum* while that of Bailey (1881, 1883, Qd Fl. 1080 (1901)) refers principally to *S. nodiflorum* subsp. *nutans*, the varietal name *humile* referring to *S. opacum*. There seems no evidence that either Brown or Bailey saw specimens of *S. nigrum* s. str. in Australia (see also discussion under *S. opacum*).

Cheel compared plants growing commonly in New South Wales especially in the Sydney district, with plants raised from seed labelled *S. opacum* received from the Botanic Gardens, Madrid, Spain. Having applied the name *S. pterocaulon* to plants of *S. opacum* and *S. nodiflorum* (see discussion under those species) he used the name *S. opacum* for the only other species well known to him in the Sydney area. This was in fact *S. nigrum*, as is the species represented by the specimen labelled by Cheel as *S. opacum* grown from seed from Spain (NSW 72026).

All but the first two specimens cited by Cheel under *S. opacum* have been examined (NSW). With the exception of *Officer's* specimen all are of *S. nigrum*. Miss Officer's plant from Hay (NSW 72032) seems to be a hybrid of *S. nigrum* since pollen ranges from 17–35 $\mu$, anthers range from 1·7–2·2 mm long, up to 4 sclerotic granules occur in the fruit and the specimen is morphologically atypical.

The presence of sclerotic granules in the fruit of Australian plants typical of *S. nigrum* has been encountered only once (Stanthorpe, *Bengston*, BRI) though in plants raised from seed from this specimen (BRI 081221) fruit set invariably lacked sclerotic granules and pollen was highly fertile in spite of

slightly irregular meiosis. In the Stanthorpe area the possibility of hybridization with sympatric diploid *S. nodiflorum* subsp. *nutans* cannot be eliminated. Such crosses between plants with differing ploidy levels are unlikely though possible (see under *S. scabrum*). The situation is perhaps comparable to that encountered by Stebbins & Paddock (1949) in California where fruits of *S. nigrum* though predominantly lacking sclerotic granules occasionally have one or two small ones.

Some as yet undetermined factor(s) of the environment appear(s) capable of inducing malformation of plants of *S. nigrum*. The leaves become reduced in size with tips conspicuously attenuate, the petals and to a less extent sepals become linear and the anthers are reduced in length and width (down to about 1·3 mm long and 0·6 mm broad). Such states have been noted in some herbarium specimens and observed in the field in South Australia. These modifications could conceivably form the basis of a variety had they not been observed on branches of plants otherwise characteristic of the species. It seems significant that Wessely (1960, p. 298) considered *S. stenopetalum* (Doell) A.Br. (*S. nigrum* var. *stenopetalum* Doell) probably only a teratological narrow-leaved state of *S. nigrum*.

CYTOLOGICAL OBSERVATIONS.—Mitosis in root-tips and tapetal tissue and meiosis in pollen mother cells in Australian plants in the field and in a series of plants grown under glasshouse conditions from seed from Queensland, South Australia, New Zealand and U.S.S.R. (Table 1) show that they have a somatic chromosome number of 72 which is that generally accepted for this species.

At meiosis, synapsis was very regular with 36 bivalents nearly always formed. In no instances were associations greater than 2 observed though in at least one cultivated plant a pair of univalents was formed in some cells. Separation of chromosome pairs was usually quite regular and daughter cells of each tetrad contained 36 chromosomes in all instances, despite some lagging observed in some cells. Each chromosome of the six genomes of the plants studied appears therefore to have but one homologue, though quadrivalent (and octavalent) associations have been reported in a postulated haploid derivative that occurred in a natural hexaploid population of *S. nigrum* in India (Rai, 1959).

Regular meiotic behaviour in these hexaploid Australian plants of *S. nigrum* tends to support the supposition of evolution of the species though alloploidy by the method suggested by Tandon & Rao (1964) rather than that suggested by Stebbins (1950).

POSSIBLE CENTRE OF ORIGIN OF THE SPECIES.—Some doubt exists as to the centre of origin of the species *S. nigrum*. By its relatively rare occurrence in the American continents, a Eurasian origin has been suggested. As stated previously the species appears best adapted to a mediterranean type of climate

suggesting that it may have come from the Middle East or even India. The work of Tandon and Rao (1.c.) would seem to support this supposition. They reported that by doubling the chromosomes of a triploid derivative of cross-pollination of what they called diploid black-fruited and tetraploid red-fruited forms of *S. nigrum,* they produced a plant morphologically identical to the hexaploid Indian form. This evidence is noteworthy in the light of Stebbins's suggestion (1950) that the karyotype of *S. nigrum* most likely contains 4 genomes of diploid *S. nodiflorum* or some other species closely related to it, and two from some diploid species as yet not identified.

Though the species seems to have arisen through hybridization, it has existed in its present form many centuries. Baranov's figure (Baranov, 1967) leaves no doubt that *S. nigrum* was known in Manchuria in the 15th century by the Chinese who used it as a wild (native) vegetable. Central Asia is also where the lectotype of the species is presumed to have been collected.

According to Gerard (1598) garden nightshade was a well-known vegetable and weed of horticulture in Britain in the 16th century though from his illustration (p. 267) it is not possible to be positive of the identity of his plants.

**Solanum nodiflorum** Jacq. Coll. 2:288 (1789); Ic. Pl. Rar. 2:11, t.326 (1789); Beadle et al. Fl. Sydney Region 488 (1972); Willis, Hbk Pl. Vict. 2:550 (1972). Type: cultivated Vienna, hb. Jacquin (lectotype BM, not seen, photo BRI).

Synonymy—see under subspecies.

Short-lived perennial, herbaceous or somewhat shrubby, erect, ascending or wide-spreading, up to 1·5 m tall. Stems bright green to wholly deep purple, angled or ± narrowly winged by the decurrent leaves or becoming terete with age, ridges or wings smooth or with widely spaced, short erect hairs, prickle hairs or obtuse soft pricklets (teeth of other authors) developed to varying degrees, not prominent on older stems, quite glabrous or sub-glabrous (rarely pubescent), hairs strongly curved, eglandular. Leaves light bright green to dark green to wholly purplish-green; blades ovate to narrowly ovate to elliptic, acute or obscurely obtuse, cuneate or somewhat abruptly contracted or sometimes almost truncate at the base, (2–)3–9(–18) cm long and (1·5–)2·5–3·5(–12) cm broad, entire, sinuate to irregularly lobed or regularly lobed or toothed, lobes when present, short, obtuse and antrorsely directed, up to 8 on each margin, surfaces glabrous or sparsely pilose to pubescent, with strongly curved eglandular hairs; petioles 1–4(–12·5) cm long, narrowly winged. Inflorescences 3–9(–12)-flowered, occasionally leaf opposed; peduncle simple or rarely forked, erect or ascending, 0·6–1·8 cm long in flower, 1–4·5 cm in fruit; rhachis condensed, internodes inconspicuous (rarely lower-most conspicuous); pedicels decurved to erect in

flower, erect to decurved to pendulous in fruit when 1·8–2·5 (–3·0) cm long. Flowers 6–8(–12) mm diam. Calyx in flower campanulate, up to ± 2 mm long, in fruit somewhat enlarged with the lobes strongly reflexed; lobes semi-elliptic, acute or obtuse, 0·4–1·2 mm long and 0·5–0·9 mm wide in flower, in fruit up to 2·2 mm long and 1·5 mm wide, glabrous or sparsely pilose outside, hairs strongly curved eglandular. Corolla stellate, white sometimes suffused with purple, rarely completely lilac; lobes 5(–8), narrowly ovate to ovate acute, 2·5–4 mm long and 1·6–2·5 mm wide, glabrous except for a small area of soft hairs on the upper outer surface and the ± fimbriate upper margins. Stamens 1·7–2·5 mm long; filaments spreading hairy on the inner side; anthers 1·2–1·6(–1·8) mm long; pollen (15–)18–23(–25) $\mu$ across. Style straight or obscurely sigmoidal, spreading-hairy in the lower $^2/_3$, 2–3·6 mm long; stigma 0·2–0·4 mm across, level with the tips of the anthers or protruding by up to 0·8 mm. Mature fruit globose or slightly depressed, purplish-black, opaque, highly glossy, 6–8(–9) mm long and 7–9(–11) mm wide, sclerotic granules absent or up to 8, when present $<$ 0·6 mm across and placed usually equatorially and occasionally also at the apex; seeds 50–80(–110), 1·4–1·6 mm long and ± 1·2 mm wide. Chromosome number: 2n(2x) = 24. Infructescence—Plate 7 (H) & (I).

The species is represented in Australia by two subspecies. Subspecies *nutans* (probably native) is distinguished from subspecies *nodiflorum* (introduced) principally by the fruiting pedicels always decurved and the presence of sclerotic granules in the fruit. Hybrids occur naturally where these subspecies are sympatric. Consequently, the combination of diagnostic subspecies characters is often lost in F1 plants and F2 or later filial selfed or back-crossed progeny.

### (a) **Solanum nodiflorum** subsp. **nodiflorum**

*S. americanum* Mill. var. *nodiflorum* (Jacq.) Edmonds, J. Arnold Arb. 52:634 (1971). Based on *S. nodiflorum*.

QUEENSLAND.—MORETON DISTRICT: Botanic Gardens, Brisbane, Nov 1917, *C. T. White* [NSW 71987] (NSW), in 1963, *Hayes* 29 (BRI), Oct 1964, *Henderson* s.n. (BRI), Jun 1967, *Henderson* 260 (BRI); Brisbane, Nov 1956, *Jones* 238 (h) (CANB, NSW); Russel I., Moreton Bay, May 1959, *Everist* (BRI); 27° 30′ S, 153° 00′ E, Indooroopilly, Brisbane, Jul 1963, *Beckman* (BRI), *Henderson* 36, 37, 38 (BRI), Jul 1968, *Dowling* (BRI), May 1970, *Henderson* 544 (BRI); Long Pocket Rd., Brisbane, Jul 1963, *Beckman* (BRI); Salisbury, Brisbane, Aug 1967, *Henderson* 299 (BRI); Acacia Ridge, Brisbane, Aug 1969, *Henderson* 521 (BRI); 27° 30′ S, 153° 00′ E, Toowong, Brisbane, Aug 1969, *Henderson* 522, 523 (BRI); 27° 05′ S, 153° 10′ E, Bellara, Bribie I., Jan 1971, *Henderson* 551 (BRI). WIDE BAY DISTRICT: 26° 25′ S, 153° 04′ E, Noosaville, Jan 1970, *Henderson* 526 (BRI). DARLING DOWNS DISTRICT: 28° 02′ S, 152° 24′ E, Cunningham's Gap, ca 45 km NE of Warwick, Mar 1973, *Henderson* 1414 (BRI).

The species was described as native to Mauritius though the lectotype is from a plant cultivated in Vienna from seed of unknown origin. In Australia subspecies *nodiflorum* is restricted to south-east Queensland between latitudes

approximately 26° to 28° S (Fig. 5). It appears a relatively recent introduction since the earliest Australian specimen examined was collected only in 1917. However the actual date and mode of its introduction remain unknown though Bailey (1881) noted that during the rush of people to the Victorian goldfields in the 1850's, persons coming from Mauritius brought seed of what he called *S. nigrum,* to grow as vegetables about their camps.

Subspecies *nodiflorum* appears to be native to the western Indian Ocean regions (e.g. Mauritius and the Seychelles), possibly the western coast of Africa, northern regions of South America, Central America including the West Indies (according to Edmonds's description, 1971) and the south eastern United States. I have seen specimens of this subspecies from Brazil (*Rambo* 40691, NSW) and Costa Rica (*Heiser* 3727, IND) and plants grown from seed (ex *Heiser*) from Ecuador (*Henderson* 356, BRI) are conspecific with plants of subspecies *nodiflorum* in Queensland.

**(b) Solanum nodiflorum** subsp. **nutans** R. J. Henderson, subspecies nova ab subsp. nodifloro foliis maturis serrato-dentatis vel sinuato-lobatis, pedicellis fructiferis semper nutantibus, granis scleroticis 1–8 in baccam omnem differt. Typus: *Henderson* 518 (holotypus BRI 086633; isotypi distribuendi—K, NSW, MEL).

? *S. photeinocarpum* Nakam. & Odash. J. Soc. Trop. Ag. 8:54 (1936). Type: Taiwan, *Odashima,* hb. Tanaka nos. 17720, 17721 (holotype or syntypes (?), TAI, not seen).

*S. allanii* Polgár, Trans. R. Soc. N.Z. 69:278 (1940). Type: Plants from seed no. 2, 3, 6, 8 & 9, on Lava fields, Mt. Wellington, Jan 1938, *Moore,* hb. Polgár(syntypes loc. ?, not seen; isosyntypes CHR, photos BRI).

*S. pachystylum* Polgár, (loc. cit.). Type: Mt. Wellington, near Auckland, Jan 1938, *Allan,* hb. Plant Research Station, Wellington, no. 8954 (holotype CHR, photo BRI).

MISAPPLIED NAMES:

*S. nigrum* auct. Aust. plur. non L.; Benth. Fl. Aust. 4:446 (1869); F. Muell. Fragm. 6:145 (1868); F. M. Bail. Qd Fl. 1079 (1901); Domin, Biblioth. Bot. 89:572 (1928).

*S. nigrum* L. var. *pterocaulon* Domin, Biblioth. Bot. 89:573 (1928).

*S. pterocaulon* auct. non Dun.; Cheel, Proc. Linn. Soc. N.S.W. 42:595 (1917).

? *S. astroites* auct. non Forst. f. nec Jacq. f.; Cheel (loc. cit.).

QUEENSLAND.—COOK DISTRICT: South Johnstone, Mar 1938, *Langdon* 6024 (BRI); Innisfail, Aug 1945, *Flynn* NSW 71965 (NSW); Mareeba, Oct 1949, *Bacon* (BRI), Oct 1967, *Cunningham* (BRI); Atherton, Jul 1963, *Cunningham* (BRI), Mar 1971, *Henderson* 563, 564 (BRI); N of Laura, May 1967, *Symon* 4779 (ADW, BRI); 15 miles SW of Mareeba, Oct 1967, *Cunningham* (BRI). NORTH KENNEDY DISTRICT: Charters Towers, Jun 1892, *Bailey* [NSW 72036] (NSW), without date, *Plant* 59 (NSW, BRI); Proserpine, Dec 1919, *Michael* 694 (in part) (BRI); Ross R., Oonoonba, Townsville, Nov 1960, *Hall* (BRI); Ravenshoe, May 1967, *Symon* 4879 (ADW, BRI); Millstream Falls, W of Ravenshoe, May 1967, *Symon* 4880 (ADW, BRI); 19° 49′ S, 146° 05′ E, Gainsford Stn., ca 40 km NW of Charters Towers, Oct 1971, *von Wald* (BRI). SOUTH KENNEDY DISTRICT: Eungella Ra., W of Mackay, Sep 1938, *White* 12973 (BRI); Mackay, Aug 1968, *Jackes* (ADW, BRI). LEICHHARDT DISTRICT: Theodore Irrigation area, Theodore, May 1958, *Gresham* (BRI). PORT CURTIS DISTRICT: Rockhampton [ca 1860] *O'Shanesy* (MEL), Jul 1865, *Dietrich* 1523 (MEL); Neerkol Ck., *Bowman* (MEL); Mt. Etna, Oct 1958, *Tracey* (ADW); Rossmoya, Rockhampton, Jul 1961, *Pembroke* (BRI); Fairfax I., Bunker Group, Nov 1927, *Rodway* [NSW 71895] (NSW); Capricorn I., Jan 1932, *MacGillivray* (BRI); Heron I., Capricorn Group, Dec 1960, *Slater* 45 (CANB); Smaller Cay, Fairfax I., Jan 1965, *Cribb* (BRI); Lady Musgrave I., Nov 1966, *Curtis* L6 (BRI); [23° 30′ S, 152° 08′ E], One Tree I., Capricorn Group, ca 59 miles ENE of Gladstone, Jul 1968, *Heatwole* (BRI); 23° 17′ S, 151° 42′ E, North West I., Aug 1968, *Baxter* 1010 (BRI). WIDE BAY DISTRICT: Gympie, *Kenny* (BRI); Wolvi Rd., Wolvi, Oct 1956, *Henry* (BRI); Boreen Pt., Lake Cootharaba, ca 20 miles (32 km) ESE of Gympie, Jan 1970, *Henderson* 530 (BRI); Long Flat, Gympie, Feb 1970, *Johnson & Fisher* (BRI); 25° 12′ S, 153° 12′ E, Eli Ck., Fraser I., May 1967, *Baxter* 815 (BRI). DARLING DOWNS DISTRICT: "Neweena", Yelarbon, Jun 1962, *McNee* (BRI); "Tanoni", Tara district, Jul 1962, *Brands* (BRI); 10 miles N of Chinchilla, May 1967, *Symon* 4779 (ADW). MORETON DISTRICT: Indooroopilly, Brisbane, Jun 1889, *Simmonds* (BRI), Jun 1968, *Baxter* (BRI); South Brisbane, Jun 1889, *Simmonds* (BRI); Brisbane R., Mar 1915, *White* [NSW 72037] (NSW); Botanic Gardens, Brisbane, Nov 1917, *White* [NSW 71987] (NSW); Mt. Glorious, Brisbane, Jun 1918, *Bick* (BRI); Hercules Bank, mouth of Brisbane R., Brisbane, Jul 1930, *White* 6909 (BRI); Main Ra. between Spring Bluff and Murphy's Ck., Aug 1930, *Hubbard* 3535 (BRI); Petrie, 18 miles N of Brisbane, Apr 1931, *Blake* 2390 (BRI); Caloundra, Aug 1932, *Cribb & Kirke* in *Blake* 4191 (BRI); Mt. Roberts, McPherson Ra. May 1951, *Johnson* 49 (NSW); Belmont, Brisbane, Sep 1956, *Everist* 5606 (BRI); Brisbane, Oct 1956, *Jones* 238(h) (NSW); Lilydale, Helidon, May 1961, *Brassington* (BRI); Lower Toowong Park, Brisbane, Jun 1963, *Beckman* (BRI); Bunya, via Ferny Grove, Brisbane, Jul 1963, *Pedley* (BRI); Morningside, Brisbane, Jan 1964, *Henderson* 47 (BRI); Coolum Research Station, Coolum, Nov 1964, *Smith & Knowles* 12219 (BRI); University grounds, St. Lucia, Brisbane, Nov 1966, *Jones* 3317 (CANB); Benarkin State Forest, Blackbutt, Aug 1967, *Henderson* 280, 281 (BRI); Helidon Hills, Sep 1968, *Baxter* (BRI); Moogerah Dam, ca 54 miles (87 km) SW of Brisbane, Jun 1969, *Henderson* 508, 512 (BRI); Caboolture, Dec 1969, *Baker* (BRI); 28° 18′ S, 152° 55′ E, Levers Plateau on Qd/N.S.W. border, ca 90 km SSW of Brisbane, Apr 1972, *Henderson* 1300 (BRI). UNPLACED: Queensland, [ca 1847], *Leichhardt* [NSW 71979 (in part), NSW 71975 (in part)] (NSW). CULTIVATED: Indooroopilly, Brisbane (seed ex Gympie, Feb 1970, *Johnson & Fisher*), Mar 1971, *Henderson* 559 (BRI).

NEW SOUTH WALES—NORTH COAST: Allyn River, Aug 1906, *Boorman* NSW 67713 (NSW); [ca 29° 00′ S, 153° 06′ E], Broadwater, Sep 1916, *Cheel* NSW 72021 (NSW); Wollongbar Experiment Farm, Wollongbar, Dec 1916, *Haywood* 3 (NSW); Leeville, Casino, Jul 1923, *Perry* 2 (NSW); Tregeagle, Mar 1946, *Chadwick* NSW 1200 (NSW); Wollongbar, Aug 1952, *Crofts* NSW 71912 (NSW); Mt. Glennie, McPherson Ra., Jan 1953, *Constable* NSW 22181 (NSW); Grafton, May 1953, *O'Grady* NSW 71906 (NSW); Byron Bay, Jun 1965, *Yabsley* NSW 78650 (NSW); Nelson Bay, Nov 1965, *Lithgow* 246 (NSW); SW shore

of Wallis Lake, SW of Forster, Jan 1967, *Salasoo* NSW 101144 (NSW); Seal Rocks, Aug 1968, *Rodd* 690, 691 (ADW); [ca 28° 35′ S, 153° 00′ E], near Kyogle, Mar 1969, *Wright* (BRI); 28° 30′ S, 152° 45′ E, Toonumbar State Forest, ca 26 km NW of Kyogle, Feb 1972, *Henderson* 1262 (BRI); 30° 55′ S, 153° 05′ E, Smoky Cape, Jan 1973, *Henderson* 1405 (BRI). CENTRAL COAST: Parsley Bay, [1800–1810], *Caley* (BM); Sydney, in 1830, *J. D. Hooker* (K); Mulsons Ferry [Milsons Ferry], Aug [1842], *Leichhardt* [NSW 71978] (NSW); North Shore, Sydney, Jun 1904, *Dixon* NSW 71913 (NSW); Ashfield, Jan 1908, Dec 1916, Nov 1932, *Cheel* NSW 71904, NSW 71916, NSW 71941 (in part) (NSW); Gooseberry I., Apr 1912, *Cheel* NSW 71936 (NSW); Hunters Hill, Aug 1912, *Carne* NSW 71903 (NSW); Woy Woy, Oct 1916, *Cheel* NSW 67712 (NSW), *Cheel* (BRI); Neutral Bay, Mar 1916, *Cleland* [NSW 72039] (NSW); Sans Souci, Sep 1916, *Goode* 346 (NSW); Parramatta, Sep 1916, *Cheel* NSW 67711 (NSW); Woonona near Bulli, Feb 1918, *Cheel* NSW 71925 (NSW); Cronulla, May 1918, *Cheel* NSW 71918 (NSW), Sep 1952, *Loaney* NSW 71929 (NSW); Pennant Hills, Jan 1919, *Steel* NSW 71926 (NSW); Epping, Apr 1921, *Henry* NSW 71915 (NSW); Ball's Head, Apr 1928, *Black* (MEL); Nielson Park, Port Jackson, Apr 1933, *Rodway* [NSW 71885] (NSW); Austinmer, Jul 1933, *Rodway* [NSW 71886] (NSW); Cowan Ck., Cowan, Mar 1938, *Blakely & Shiress* NSW 67710 (NSW); near Bellawangra, Cambewarra Ra., Oct 1939, *Rodway* [NSW 71898] (NSW); West of Pennant Hills, May 1945, *Johnson* NSW 71922 (NSW); Shellharbour, Nov 1949, *McBarron* NSW 71910 (NSW); Broughton Pass, Lower Cataract R., May 1951, *Johnson* NSW 71919 (NSW); Eastwood to Denistone, Nov 1952, *Evans* NSW 72023 (NSW); Cheltenham, Feb 1954, *Johnson* NSW 71920 (NSW); Maroubra, Nov 1954, *Ford* NSW 71928 (NSW); Ashton Park, Sydney, Apr 1956, *Baylis* S53 (AD); Scarborough Park, Kogarah, Jan 1965, *Constable* 5633 (NSW); Bouddi Ra., Dec 1965, *Whitehead* (ADW); Wyong, May 1966, *Whitehead* (ADW). SOUTH COAST: Montague I., Apr 1932, *Rodway* [NSW 71899] (NSW); Huskisson, Jervis Bay, May 1934, *Rodway* [NSW 71891] (NSW); Bowen I., Jervis Bay, Jun 1934, *Rodway* [NSW 71892] (NSW); Brush I., Aug 1936, Sep 1936, *Rodway* [NSW 71888, NSW 71889] (NSW); Tabourie I., Jan 1940, *Rodway* [NSW 71901] (NSW); South Crookhaven Head, Jan 1941, *Rodway* [NSW 71900] (NSW); North I. of Tollgates, Bateman's Bay, Dec. 1958, *Warner* 32 (CANB); Ohlsons Ck. near Narooma, May 1964, *Willis* (MEL). CENTRAL TABLELAND: Jenolan Caves, Feb 1900, *Blakely* NSW 71939 (NSW); Hill Top, S of Sydney, Jan 1915, *Cheel* NSW 71911 (NSW), Jan 1915 *Boorman* (BRI).

VICTORIA.—CENTRAL DISTRICT: Banks of Latrobe R., Noojee, Dec 1963, *Willis* (MEL). WESTERN DISTRICT: Near Ararat, without date, *Green* (MEL).

NORTHERN TERRITORY.—DARWIN & GULF DISTRICT: 13° 15′ S, 131° 07′ E, Adelaide River farms, Sep 1972, *Holmes* (BRI). VICTORIA RIVER DISTRICT: Victoria River, [ca 1850], *Mueller* (MEL).

WESTERN AUSTRALIA.—SOUTH-WEST PROVINCE: Stirling District—Mount Many Peaks R., *Maxwell* (MEL); Bald I., *Maxwell* (MEL). Warren District—12 miles N of Busselton, Sep 1965, *Beauglehole* 12438 (ADW). Darling District—Perth, Apr 1898, *McKaige* (PERTH); Bibra Lake, Nov 1961, *George & Marchant* 3172 (in part) (PERTH); South Perth, Jan 1968, *Royce* 8404 (PERTH, ADW).

Subspecies *nutans* occurs commonly in coastal and near coastal localities in eastern Australia and on closely adjacent islands (Fig. 3) and is considered native to these areas. It was collected at an early date in south-western Western Australia and in north-western Northern Territory but, based on present day occurrences, appears to be an introduction to these regions.

This subspecies also occurs on Lord Howe Island (NSW, K), Norfolk Island (BRI), in the Fijian Islands (BRI), New Zealand (CHR, MEL, NSW), lower altitudes of New Guinea and associated islands (BRI) and probably in countries in the north-western Pacific Ocean region (from Nakamura, 1937). Results of Baylis's cross-breeding experiments with New Zealand plants of this subspecies and plants of Californian origin indicate that it also occurs in regions bordering the eastern Pacific Ocean.

Paddock's specimens from California and Oregon (*Paddock* 161, 166, UC) seem to be of subsp. *nutans* as do those of Eichler's from California (*Eichler* 20503, AD). The illustration of *S. nodiflorum* given by St. John and Hosaka (1932) for Hawaiian material undoubtedly refers to subsp. *nutans*. A detailed study of these taxa in western regions of the Americas should establish the exact taxonomic position. The detailed results of cytogenetic investigations of this group in Pacific North America promised by Stebbins and Paddock (1949), appear still unpublished.

The protologue of *S. nodiflorum* applies to plants in the neighbourhood of Brisbane. Examination of a photograph of the type specimen (Plate 1) shows that application of this name to these Queensland plants is justified. According to Baylis (1958) the diameter of pollen from the type, mounted in lacto-phenol is 23 $\mu$ which is considered to indicate that the specimen is from a diploid plant. The Queensland plants are diploid and have pollen of similar dimensions (Fig. 1). On the basis of his studies of New Zealand species, on herbarium material of plants from near Sydney and the illustrations of Cheel (1917), Baylis considered *S. nodiflorum* occurred in Australia. Examination of his material (AD) and Cheel's plates 31 and 32a–b, shows that he was referring to a taxon closely related to though not identical with that identified as *S. nodiflorum* near Brisbane. However, on the basis of their numerous morphological similarities, the existence of a partial barrier to their cross-breeding (as discussed later) and a supposed natural allopatric distribution, these two taxa are considered subspecies of *S. nodiflorum*.

Edmonds (1971, 1972) reduced *S. nodiflorum* Jacq. to varietal rank under *S. americanum* Mill. on the grounds that she considered the lectotype of each conspecific. The protologue of *S. americanum* appears to apply specifically to plants of *S. nodiflorum* subsp. *nodiflorum* but the specimen chosen by Edmonds to typify *S. americanum* (ex hb. Miller (BM), Plate 3) does not agree with any in Australia. These lectotypes are compared in Table 2. In the absence of any further material for consideration it seems preferable to maintain *S. nodiflorum* for Australian plants agreeing with Jacquin's specimen (Plate 1). Though individuals of the taxon here named subsp. *nutans* match neither type, the taxon's affinities with subsp. *nodiflorum* are considered clearly demonstrated by the results of the biosystematic crossing programme discussed on page 37.

TABLE 2

COMPARISON OF CERTAIN CHARACTERS OF THE LECTOTYPES OF *SOLANUM AMERICANUM* MILL. AND *S. NODIFLORUM* JACQ. MAINLY FROM PHOTOGRAPHS.

| Character | *S. americanum* | *S. nodiflorum* |
|---|---|---|
| Flowers per peduncle | — 9 | — 6 |
| Anther lengths | from "ca. 1·8"* to 2 mm | 1·2 mm† |
| Pollen size range in $\mu$ in lacto-phenol-aniline blue | prolate 25·8 x 17·2 — 25·8 x 19·3‡ prolate spheroidal 21·5 x 17·2 — 23·6 x 21·5 (measurements as high as 27 in Mikrops) | ca. 23§ |
| Form of infructescence | racemiform | umbelliform |
| Fruiting pedicels | decurved to pendant | divaricate (erect to spreading) |
| Fruit per peduncle | 6–8 | 4–5 |
| Flattened fruit size | 6–7 mm diam. | 3·5–4 mm diam. |

* Measured by Dr. W. T. Stearn (BM).

† Measurement made by G. Chippendale while Australian Botanical Liaison Officer at K, 1972–1973.

‡ Measurements made by Mrs. Shukla Sengupta at BM.

§ Measurements reported by Baylis, 1958.

The basis for Edmonds's record of *S. americanum* var. *americanum* and var. *nodiflorum* in Australia is not known.

Though neither type material of *S. photeinocarpum* Nakamura & Odashima nor material cited as *S. photeinocarpum* by Nakamura (1935, 1937) has been seen, the description and photographs of their plants leave little doubt that they were referring to plants of *S. nodiflorum*. The attitude of the fruit in Nakamura's plate strongly suggests that their name refers to subsp. *nutans*.

Examination of five of the isosyntypes of *S. allanii* Polgár (CHR) shows that as Baylis suggested the specimens belong with *S. nodiflorum*. They are however referrable to subsp. *nutans* by the nature of the infructescence and presence of sclerotic granules in the fruit. The characters listed by Polgár to distinguish *S. nodiflorum* from his plant, are those of subsp. *nodiflorum*. The series of specimens on which *S. pachystylum* is based (CHR) is a mixture of *S. nodiflorum* subsp. *nutans* and *S. nigrum*. However from the protologue the name appears to refer to the specimens of *S. nodiflorum* subsp. *nutans* which are showing the effects of senescence and are not morphologically typical of the subspecies.

Both subspecies have passed under the name *S. nigrum* in literature on Australian plants. Bentham, Mueller, Domin and F. M. Bailey cited or identified by description specimens of *S. nodiflorum* as *S. nigrum*. These mostly refer to subsp. *nutans* though Bailey did not distinguish between the two subspecies, if both were present near Brisbane before 1917.

It is evident from the protologue to *S. pterocaulum* that Dunal considered he was giving a name at species level to the plant known by the pre-Linnean name *Solanum nigrum, vulgare simile, caulibus exasperatis* (Dillenius Hort. Elth. 367, t.275, f.356, 1732). Dunal's name though validly published is illegitimate being a superfluous name for *S. scabrum* Mill. (ICBN Art. 63). In the protologue Dunal spelt the specific epithet with the latin termination *-um,* but changed it to greek *-on* later in his account of *Solanum* in De Candolle's Prodromus. This later spelling appears to have been used by all subsequent authors. Since there is no obstacle to its use the original spelling "pterocaulum" should be used (ICBN Art. 73).

Since Linnaeus (Sp. Pl. ed. 1:186, 1753) based *S. nigrum* var. *virginicum* on Dillenius's description and plate, Dunal included it in synonymy under *S. pterocaulum.* It seems obvious that his record of this species from Australia ("[Pt.] Jackson, et littoribus inter tropicum") in the protologue, is based solely on Brown's note that he considered Australian plants were of *S. nigrum* L. $\epsilon$ [= var. *virginicum* L.] (Prod. Fl. Nov. Holl. p. 445, 1810), since it is doubtful that Dunal had seen by that time any specimens Brown collected in Australia. This is further discussed under *S. opacum.*

Domin made the combination *S. nigrum* var. *pterocaulon* on the basis of Dunal's illegitimate *S. pterocaulon* of 1852, apparently without reference to any of his specimens. By so doing, Domin's subsequent citation of two specimens of *S. opacum* (Gilbert River, *Mueller* and Port Curtis, *MacGillivray* (K)) and one of *S. nodiflorum* subsp. *nutans* (Sydney, *Hooker* (K)) as belonging to *S. nigrum* var. *pterocaulon* is a misapplication of that name.

It seems certain that on the basis of Dunal's and Don's record (see under *S. opacum*) of this species from Australia, Dillenius's plate and Brown's specimen from Broad Sound (NSW), Cheel applied the name *S. pterocaulon* to Australian plants with ". . . branches . . . with distinctly winged angles or margins, the winged margins minutely but distinctly jagged so that they appear somewhat serrulate or prickly, as seen in Plate 33, fig. a. The leaves . . . more or less crenate-sinuate. Flowers . . . on slender pedicels, usually in threes or rarely four or more in the raceme. Berries at first green, afterwards shiny black . . ." The description applies almost exclusively to *S. nodiflorum* subsp. *nutans* as

does Plate 31 in his paper. Examination of some of the specimens cited by him (7) and others collected and determined by him shows that this is the species to which he was referring. However, since Cheel was unable to distinguish between it and *S. opacum* s. str., he included specimens of both under the name *S. pterocaulon*.

On the basis of plants raised from seed labelled *S. astroites* Forst. received from the Botanic Gardens, Madrid, Cheel applied that name to a number of specimens including one he collected from Broadwater, northern New South Wales. *S. astroites* Forster is a nomen nudum and hence invalid. Since there is also no evidence that Cheel saw any material available to Forster, the name, at least in this Australian context, is attributable solely to Cheel. The specimen of Cheel's plant raised under number 31 (NSW), is not of any species at present occurring in Australia so that in effect, his use of *S. astroites* for the plant he collected from Broadwater, New South Wales, is a misapplication of the name. This specimen (NSW) clearly belongs with *S. nodiflorum* and is probably of subsp. *nutans* though the material is insufficient for positive identification.

Type material of *S. oleraceum* Dun. (Dunal in Poir. Suppl. 3:750, 1814) is from Central America and north-eastern areas of South America and is generally regarded as belonging to *S. nodiflorum*. Although the majority of specimens referred to *S. oleraceum* by Dunal in 1852 seem to be of *S. nodiflorum* the specimen on which he based his record of the species for Australia is not readily identifiable from the microfiche (IDC 800–61.2062:III.8). In the absence of anther and pollen grain measurements it seems to be of *S. opacum* or possibly of *S. nodiflorum* subsp. *nutans*.

Though specimens cited by Seeman (1863) have not been seen, it seems that his statement that he had seen *S. oleraceum* about Sydney is most likely based on plants of *S. nodiflorum* subsp. *nutans* or *S. opacum*.

There are specimens from the Philippine Islands and Sumatra (BRI) which, though possessing anthers and pollen characteristic of a diploid agree more with *S. nigrum* in the larger flowers and racemiform nature of the infructescence. These specimens may be referable to the atypical form of *S. photeinocarpum* noted by Nakamura (1937), though none of his specimens has been available for comparison. It seems that plants of this group are in need of detailed study in south-east Asia.

CYTOLOGICAL OBSERVATIONS.—The chromosome complement of all Australian plants of both subspecies and hybrids (artificially produced and supposedly natural) examined cytologically was 24. This was determined from both meiosis in pollen mother cells and mitosis in root tips and occasionally tapetal

tissue in material collected from numerous volunteers in the field and plants grown from seed under glasshouse conditions. Apart from instances listed in Table 3, bivalent formation at meiosis was regular in every individual studied and daughter (tetrad) cells always contained 12 chromosomes. Only representative counts are recorded in Table 1. Failure of a small number of chromosomes to pair during Prophase I seemed the principal manifestation of irregular meiosis in certain artificially produced F2 hybrid individuals (Table 3), though trivalent formation was noted on rare occasions. However, daughter cells appeared always to contain normal haploid chromosome numbers in spite of these irregularities.

It is interesting to note that seed received from the Vilar Institute, U.S.S.R. and labelled *S. nodiflorum* Jacq. produced plants with morphological characteristics of *S. nodiflorum* subsp. *nodiflorum* but with a somatic chromosome number of 72, the hexaploid level in the species. This particular line is probably the same as that for which Gerasimenko & Reznikova (1968) recorded a somatic number of 72 for *S. nodiflorum* and is probably only of rare occurrence in the species as a whole.

BIOLOGICAL OBSERVATIONS AND CROSS-BREEDING EXPERIMENTS.—In an attempt to explain the diversity of forms of *S. nodiflorum* near Brisbane a limited cross-breeding programme using what appeared to be characteristic representatives of the two major types (recognised as subspecies in this paper) was devised. The results, a synopsis of which is shown in Table 3, clearly indicate that two cytodemes are established in the area. As the barrier to gene flow between them though strong is incomplete, introgression has occurred near Brisbane. Here back-crossed progeny displaying morphological segregation obscures expression of the parental genotypes.

Further results of this crossing programme are noteworthy as they shed light on the breeding behaviour within this and probably related species. As stated previously, plants are predominantly self-pollinating, sexually reproducing individuals. Some out-crossing is known to occur with other flowers on the same plant or nearby individuals but it is likely that in most instances, individuals of a population are sibling progeny of only one self-pollinating ancestor. For artificially produced hybrids it was found that back-crossing or out-crossing to other individuals was necessary at some stage for establishment of subsequent progeny and as such probably helps to reduce the occurrence of natural hybrid offspring where different species are closely associated. Bagged self-pollinated flowers of artificial F1 hybrids set few well filled seed. Only a small percentage of this seed germinated and resultant seedlings were sickly and died prematurely. A fair proportion of F2 progeny failed to set fruit even when provided with the opportunity of cross-pollination.

TABLE 3
SYNOPSIS OF RESULTS ON CERTAIN CHARACTERS FOLLOWING RECIPROCAL CROSS-BREEDING EXPERIMENTS WITH SUBSPECIES OF *SOLANUM NODIFLORUM*

| CHARACTER | PARENT | | FILIAL 1 | | FILIAL 2 | | |
|---|---|---|---|---|---|---|---|
| | subsp. *nodiflorum* field | subsp. *nutans* field | Artificial glasshouse | Putative field | ex putative F1 glasshouse | Artificial | |
| | | | | | | Glasshouse | Field |
| Margins of adult leaves .. .. | Sinuate to entire | Multidentate | 1 (–2) teeth/ margin (rarely entire) | 1 tooth/ margin or entire | Sinuate to multidentate | Entire to multidentate | Entire to multidentate |
| Percentage of viable pollen .. | 97 | 91 | 18–25 | 17–18 | 0–32 | 41–99 | 0–60 |
| Attitude of fruiting pedicels .. | Erect to pendant (Type I) | All pendant (Type II) | All pendant (Type II) | All pendant (Type II) | Type I 40%<br>Type II 60% | Type I 50%<br>Type II 50% | nr |
| No. of fruit/peduncle .. .. | 5–8 | 3–5 | 4–7 | 2–5 | 0*–8 | 0*–8 | 0*–8 |
| Diameter of ripe fruit in mm .. | 7–9 | 7–8 | 4–7 | nr | 3–7·5 | 4·5–9 | nr |
| No. of functional seed/fruit .. | (40–) 55–70 | 65–85 | 4–18 | 4–12 | 0†–30 | 0†–60 | nr |
| No. of sclerotic granules/fruit .. | 0 | (1–) 4 (–5) | 0 (1) | 0 | 0–4<br>A 33·5%<br>B 50 %<br>C 16·5% | 0–4<br>A 41%<br>B 50%<br>C 9 % | nr |
| Nature of meiosis .. .. | Regular | Regular | Regular | nr | D 33·5%<br>E 66·5% | D 83·3%<br>E 16·7% | nr |
| Voucher specimen No. .. .. | *Henderson* 299 | *Henderson* 298 | *Henderson* 1328, 1329, 1330, 1331 | BRI 081329 | *Henderson* 470–475 (6 indiv.) | *Henderson* 458–469 (12 indiv.) | 40 individuals, no vouchers kept |

* Some plants set no fruit
† Some fruits contained no seed

A no sclerotic granules in any fruits
B at least 1 sclerotic granule in at least 1 fruit
C at least 1 sclerotic granule in all fruit

D regular meiosis
E showing at least some degree of irregular meiosis
nr not recorded

All stages of meiosis in artificially produced F1 individuals were regular and daughter cells invariably contained the exact haploid number of chromosomes indicating that reduction of the amount of viable pollen observed in these plants is probably governed by a cytoplasmic factor. This may explain low pollen viabilities in otherwise typical plants in the field. Cytoplasmic determination of male fertility is a phenomenon well known to plant breeders (e.g. Warmke & Overman, 1972) and according to Edwardson (1956), has been artificially induced in tomatoes (*Lycopersicon* sp.).

Results of reciprocal crossing with the hexaploid *S. opacum* are described in discussions under that species.

**Solanum opacum** A.Br. & Bouché, Ind. Sem. Hort. Berol. App. 8:18, no. 39 (1853); C. Muell. in Walp. Annal. Bot. Syst. 5:562, no. 4 (1859). Type: cultivated Berlin, seed from Australia, *Listeman* (holotype B†; isotype(s) ?; neotype—Broad Sound, Sep 1802, *R. Brown* [NSW 125341] NSW; isoneotypes K, MEL).

*S. nigrum* L. var. *chlorocarpum* F. Muell. ex Domin, Biblioth. Bot. 89:573 (1928) *nom. nud.,* non A.Br. in Doell, Rheim. Fl. 413 (1843), nec (Spenn.) Fil. in Kult. Fl. SSSR 370–386 (1958). Based on – Murray [R.], in 1853, *F. Mueller* (K, photo BRI).

MISAPPLIED NAMES:

*S. nigrum* auct. Aust. plur. non L.; R.Br. Prod. Fl. Nov. Holl. 445 (1810); Benth. Fl. Aust. 4:446 (1869); F. Muell. Fragm. 6:145 (1868).

*S. nigrum* L. var. *humile* F. M. Bail. Trans. Phil. Soc. Qd 3:1–4 (1881); Syn. Qd Fl. 342 (1883).

*S. nigrum* L. var. *pterocaulon* Domin, Biblioth. Bot. 89:573 (1928).

*S. pterocaulum* Dun. Hist. Sol. 153 no. 33 (1813); G. Don, Gen. Syst. 4:412 (1838).

*S. pterocaulon* auct. non Dun. (1852); Cheel, Proc. Linn. Soc. N.S.W. 42:595 (1917).

*S. nodiflorum* auct. non Jacq.; Baylis, Trans. Roy. Soc. N.Z. 85:383 (1958).

? *S. oleraceum* Dun. in DC. Prod. 13,1:50 (1852).

Annual or short lived perennial, usually prostrate or procumbent or erect but becoming procumbent with age, low and spreading to about 1 m across or up to 0·75 m tall when erect. Stems deep green or sometimes streaked with purple or wholly purplish, angular or narrowly winged by the decurrent leaves, ridges smooth, sub-glabrous, pilose to densely pubescent with strongly curved or

also somewhat spreading eglandular hairs. Leaves deep green, sometimes the principal veins on the upper and especially on the lower surface outlined in deep purple; blades ovate, narrowly ovate to elliptic, acute, gradually attenuate to the petiole, 3–7(–12) cm long and 2–4·5(–6) cm broad, usually lobed often prominently but sometimes merely sinuate or almost entire, lobes widespread usually acute, 1–5 on each margin, surfaces sub-glabrous to densely pubescent with strongly curved or somewhat spreading eglandular hairs; petioles 1·5–4(–5) cm long, ± narrowly winged. Inflorescences (2–)3–4 flowered; peduncle simple, erect or ascending, ± 1 cm long in flower, sharply deflexed and 1–2·5 cm long in fruit; rhachis condensed, internode(s) inconspicuous (or rarely lowermost conspicuous); pedicels decurved or spreading in flower, pendulous in fruit when 0·8–1·5 cm long. Flowers 8–12 mm diam. Calyx in flower campanulate, 2–3 mm long, in fruit flattened and appressed to the berry, 8–9 mm diam.; lobes semi-elliptic to broadly triangular, obtuse, 0·6–1 mm long and ± 0·8 mm broad in flower, 1·5–2 mm long and 1·5–2 mm wide in fruit, glabrous or sparsely pilose outside, hairs strongly curved. Corolla stellate, white, frequently with a longitudinal purple stripe in the centre of the outside of each lobe; lobes narrowly ovate, acute, 4–4·5 mm long and ± 3 mm wide, glabrous except for a small area towards the tip on the outside and the somewhat fimbriate upper margins. Stamens 2–4·5 mm long, filaments spreading hairy on the inner side; anthers 1·2–1·7(–1·8) mm long; pollen (22–)24–28(–32) $\mu$ across. Style straight, spreading hairy in the lower $\frac{1}{2}$–$^{2}/_{3}$, 3–3·5 mm long; stigma ± 0·4 mm across, level with the tips of the anthers or protruding by up to 0·5 mm. Mature fruit globose or slightly depressed, usually green (rarely purplish), often with a narrow purplish ring round the stylar scar, opaque, dull, 8–10 mm across and 7–8·5 mm long, pulp with a decided sweet odour, sclerotic granules usually 2 (rarely 4), (0·6–)0·8–1·2 mm across at the apex only; seeds 20–40(–60), 1·8–2·2 mm long and 1·2–1·5 mm wide. Chromosome number: 2n(6x) = 72. Infructescence—Plate 6 (A). Probably native, possibly endemic.

QUEENSLAND.—COOK DISTRICT: Gilbert R. [in 1856] *Mueller* (K). NORTH KENNEDY DISTRICT: Seaview Ra., Rockingham Bay, Jun 1865, *Dallachy* (MEL); Proserpine, Dec 1919, *Michael* 694 (BRI); 18° 20′ S, 144° 55′ E, Kinrara Crater on Meadowbank Stn., McBride Plateau area, Feb 1971, *Webb & Tracey* 10256 (BRI). PORT CURTIS DISTRICT: Broad Sound, Sep 1802, *R. Brown* (K, MEL, NSW), without date, *Macartney* (MEL); Port Curtis, Nov 1847, *MacGillivray* (K); Rockhampton, Apr 1867, *O'Shanesy* 71 (MEL). LEICHHARDT DISTRICT: Dawson R., Jul 1847, *Leichhardt* [NSW 71975] (NSW); "Cluden", ca 15 miles SE of Taroom, July 1955, *Pedley & Johnson* 70 (BRI); Mt. Playfair, in 1890, *Miss Biddulph* 14 (MEL), Mar 1961, *Biddulph* 186 (BRI); 24° 35′ S, 149° 55′ E, ca 8 km E of Moura, Mar 1968, *Henderson* 396 (BRI). BURNETT DISTRICT: Burnet [t], Qld, *Haly* (MEL); Kingaroy, Apr 1947, *Smith* 3071 (BRI); Kumbia, ca 25 km SW of Kingaroy, May 1947, *Michael* 3026 (BRI); Bunya Mts. National Park, ca 30 miles SW of Kingaroy, Nov 1967, *Henderson* 302 (BRI). MORETON DISTRICT: Brookfield near Brisbane, Dec 1888, *Simmonds* (BRI); Blackall Ra., May 1910, *Keys* (BRI, NSW); Enoggera, Brisbane, May 1916, Jun 1919, *White* (BRI, NSW); Cedar Ck. near Beenleigh, Feb 1920, *White* [NSW 99823] (NSW); Wilson's Peak, Apr 1949, *White* 13009 (BRI), Feb 1968, Aug 1972, *Henderson* 359, 1341 (BRI); Kenmore, Brisbane, Jul 1960, Jan 1965, *Kleinschmidt* (BRI);

Mt. Mee ca 13 miles W of Caboolture, Apr 1967, Jun 1968, *Henderson* 246, 403 (BRI); Benarkin State Forest, ca 15 miles E of Yarraman, May 1967, *Henderson* 250 (BRI), Aug 1967, *Henderson* 285, 290, 291, 292 (BRI); Jolly's Lookout, ca 20 km WNW of Brisbane, Jun 1969, *Henderson* 514 (BRI); Woombye, S of Nambour, Dec 1971, *Wilson & partners* (BRI); 28° 18′ S, 152° 55′ E, Levers Plateau on Qld/N.S.W. border, ca 90 km SSW of Brisbane, Apr 1972, *Henderson* 1280 (BRI). DARLING DOWNS DISTRICT: "Jimba", plains of the Condamine, Sep 1844, *Leichhardt* [NSW 71979, NSW 71973] (NSW); Toowoomba, *F. M. Bailey* (BRI); Wallangarra, Apr 1924, *Cheel* NSW 71943 (NSW); Bell-Bunya Mts. road, ca 3 miles S of Mt. Mowbullan, May 1958, *Johnson* 462 (BRI); Canaga, Jun 1958, *Stewart* 8 (BRI); "Strathgarve", ca 21 miles S of Warwick, Feb 1960, *Everist* 6160 (BRI); 28° 22′ S, 152° 03′ E, ca 12 miles S of Warwick, Mar 1968, *Henderson* 394 (BRI). MARANOA DISTRICT: "Meadowbank", ca 6 miles W of Roma, May 1961, *Pope* (BRI).

NEW SOUTH WALES.—NORTH COAST: Hastings R., *Beckler* (MEL); Purgatory Ck., 7 miles NW of Ramornie, Jul 1922, *Blakely & Shiress* NSW 71996 (NSW); Girard State Forest, 3 miles W of Drake, Apr 1956, *Constable* NSW 37890 (NSW); Toonumbar State Forest, ca 26 km NW of Kyogle, Feb 1972, *Henderson* 1261 (BRI). CENTRAL COAST: New Holland, ? May 1770, ? *Banks & Solander* [NSW 99968] (NSW); Port Jackson, 1802–1805, *Brown* (BM, K); New South Wales, [1816–1824], *Field* (BRI); Parramatta, [ca 1860], *Woolls* (MEL); Kurnell, Botany Bay, May 1906, *Boorman* NSW 71923 (NSW); Christies Gully, Mooney Mooney Ck., Sep 1926, *Blakely, Darnell-Smith & Shiress* NSW 71940 (NSW); Five Is. near Wollongong, Mar 1936, *Rodway* [NSW 71886] (NSW); Bouddi Ra., near Brisbane Water, Dec 1965, *Whitehead* (ADW). SOUTH COAST: Bowen I., Dec 1931, *Rodway* [NSW 71893] (NSW); Tanja near Bega, Oct 1940, *Glenfield* Vet. Res. Stn. NSW 71997 (NSW). NORTHERN TABLELANDS: Chandlers Peak, Guyra, Mar 1917, *Boorman* NSW 71942 (NSW). CENTRAL TABLELANDS: Jenolan Caves, Feb 1900, *Blakely* NSW 71938 (NSW); Jenolan Caves Rd., Mar 1950, *Constable* NSW 11096 (NSW); Kanangra, 10 miles SE of Jenolan Caves, May 1965, *Constable* 5866 (NSW); Mt. Irvine, Apr 1970, *Burgess* (AD). SOUTHERN TABLELANDS: Heap's Gully, 3 miles SE of Bungonia, Jan 1956, *Constable* NSW 35318 (NSW); China Walls, 17 miles SE of Tumbarumba, Feb 1964, *Muir* 3244 (NSW). CENTRAL WESTERN SLOPES: Mudgee, Mar 1908, *Insp. of Stock* NSW 72001 (NSW); Barramgan beyond Mudgee, *anon.* 49 (MEL). WESTERN PLAINS: Wooloondool near Hay, Feb 1916, *Froggatt* NSW 71939 (NSW); Griffith, Apr 1943, *Fraser* NSW 72004 (NSW). CULTIVATED: Ashfield (seed ex Brisbane, Q, *White*) Jan 1921, Feb 1921, *Cheel* NSW 71962, NSW 71969 (NSW).

VICTORIA.—GIPPSLAND DISTRICT: Gabo I., [ca 1870], *Maplestone* (MEL). CENTRAL DISTRICT: Melbourne, Apr 1853, *Adamson* 51 (K); Portarlington, in 1870, *Dickinson* (MEL). WESTERN DISTRICT: Between Glen Aire and Johanna Bay, Southern Otways, Apr 1963, *Allender* (MEL). MALLEE DISTRICT: Murray R., *anon.* (MEL), ca 1855, *Herrgott* (MEL); Murray [R.], in 1853, *Mueller* (K, MEL); junction Darling and Murray Rivers, May 1887 & ca 1887, *Holding* (MEL). UNPLACED: Clear Creek dist., *anon.* 77 (MEL); Demon Ck., *anon.* (MEL).

TASMANIA.—"Port Effingham" near George Town, Jul 1843, *Gunn* 51 (NSW, BRI, K); North Bruny, Jan 1931, *Rodway* 121 (CANB); Solomons Hill, Harford, Nov 1932, *Hamilton* 163 (CANB); Burnie, hb. *Black* (MEL).

SOUTH AUSTRALIA.—KANGAROO ISLAND: Kangaroo I., *Waterhouse* (MEL).

There are in MEL specimens of *S. opacum* supposedly collected near Adelaide in 1847–1848 (MEL 11456, MEL 11459) by Mueller. This species is not known to occur there naturally. Since "V.D.L." is included on one label it is probable Mueller collected *S. nigrum* from the Mt. Lofty Ranges (one specimen on MEL 11459) and at about the same time received specimens of *S. opacum* from Tasmania (possibly a portion of the *Gunn* collection, the K specimen of which also has "V.D.L." in the same handwriting) and inadvertently mixed the collections.

Solander, in a manuscript list of specimens collected by Banks and himself in Australia made at or about the time of their collection in 1770, recorded 12 specimens of *Solanum nigrum* from St (= Stingray harbour ≡ Botany Bay). However, in manuscripts of the Australian flora prepared later (BM) he did not include *S. nigrum*. There are apparently no specimens at K or BM to support Solander's field notes though there is a specimen in NSW labelled as *S. nigrum* and collected by Banks and Solander from New Holland. This is a specimen of *S. opacum*. A portion of this specimen has been transferred to BM (MacGillivray, NSW, pers. comm.).

This species occurs in eastern and south-eastern Australia including Tasmania (Fig. 6) mainly in damp or well-watered heavy soils. Because of the date and widely separated localities of early collections (? 1770 or at least 1802–1805 from Port Jackson and Broad Sound) and the apparent confinement of the species in this form to Australia, it is considered native to these areas. It appears to be represented in New Guinea by a distinct variety or subspecies distinguishable by a tall erect shrubby habit of growth.

No original material of *S. opacum* A.Br. & Bouché has been seen. Any specimens made of the plant grown from seed from Australia and preserved in Braun's herbarium in Berlin are no longer extant according to the Director of the Botanischer Garten und Museum, Berlin–Dahlen, in correspondence. In addition the existence of any duplicate material elsewhere is unknown. In the absence of any authentic specimens, the NSW sheet of Robert Brown's collection from Broad Sound has been selected as neotype of Braun and Bouché's name. The very detailed description given in the protologue leaves very little doubt as to the correct application of the name. I have found no information about Listeman or the possible origin in Australia of his seed.

F. Mueller (Fragm. 6:145, 1868) in discussing *S. nigrum* in Australia indicated that he had seen here a variety with green fruit, though he did not formally propose a name for it. There are however at least two specimens in MEL and one in K labelled as *Solanum nigrum* var. *chlorocarpum* in Mueller's handwriting though one of the Melbourne specimens (MEL 11485) though

dated 1850 is almost certainly part of the Mueller collection (K) cited by Domin. The first formal use of the varietal epithet in Mueller's sense seems to be by Domin, but since he gave no diagnosis the name is invalid even though a specimen was cited. These specimens are all of *S. opacum*. According to Wessely (1960), *S. nigrum* L. var. *chlorocarpum* A.Br. and *S. nigrum* L. var. *chlorocarpum* (Spenn.) Fil. are taxonomic synonyms of *S. nigrum* L. var. *nigrum* forma *humile* Lindmann. Several specimens of the European plant variously identified as *S. humile* Bernh. ex Willd., *S. nigrum* L. var. *humile* (Bernh. ex Willd.) Doell or *S. nigrum* L. var. *nigrum* f. *humile* (Bernh. ex Willd.) Lindmann, have been examined (GFW). They include material examined and cited by Wessely. This taxon seems no more than a form of *S. nigrum* sens. str. as Wessely concluded and as such is specifically distinct from *S. opacum*.

It should be noted that *S. humile* Bernh. ex Willd. (1809) is illegitimate being a later homonym of *S. humile* Lam. Tab. Encyc. 2:23 (1794). The epithet *humile* at the rank of variety or forma under *S. nigrum* is therefore treated as a new name (ICBN Art. 72) so that Lindmann is the author of *S. nigrum* forma *humile*.

At the time of publishing the name *S. opacum* for plants from Australia, Braun considered Bernhardi's name referred to a different plant which he named *S. nigrum* var. *luteo-virens* in the same seed list. However, he considered this variety distinct from that he named *S. nigrum* var. *chlorocarpum*.

Brown's concept of *S. nigrum* covered the plants he collected at Port Jackson (BM) and Broad Sound (BM, NSW, MEL). Since they are all of *S. opacum* and the description given in his Prodromus seems to apply exclusively to that species also there is no evidence he saw specimens of either *S. nigrum* sens. str. or *S. nodiflorum* in Australia. Brown's use of *S. nigrum* for those plants is therefore a misapplication of that name. Bentham's and Mueller's use of the same name for plants of this species is discussed under *S. nigrum*. Most other authors have considered Australian plants of *S. opacum* as representing only forms of what they believed to be the highly variable *S. nigrum*.

Examination of plants labelled by F. M. Bailey as *S. nigrum* var. *humile* shows that he used that name for Queensland plants of *S. opacum*. The text in his paper on naturalized Solanums (Bailey, 1881) indicates that he was accepting the varietal name in the sense of some other author, but it has been impossible to establish any likely one. His description does not completely agree with Queensland plants or any other Australian plants, for to describe *S. opacum* as having ". . . the foliage . . . clothed with glandular hairs" and ". . . fruit . . . of a greenish yellow when ripe" is erroneous. Apart from a small increase in the density of the small inconspicuous stalked glands ("Drüsen" of Wessely, 1960) present on all species of this group under study, all hairs of *S. opacum* are simple

and eglandular. In the mature state, berries are almost always some shade of dull green though when in extremely ripe condition on the ground, a slight pinkish coloration may be detected in them. The epithet *humile* seems therefore to be based on some other type and the name misapplied by Bailey to Australian plants of *S. opacum.*

Domin's misapplication of *S. nigrum* var. *pterocaulon* to specimens of *S. opacum* is discussed under *S. nodiflorum.*

As stated previously, Dunal in the protologue to *S. pterocaulum* recorded this species from Australia presumably on the basis of the entry under *S. nigrum* in Brown's Prodromus without actually examining any of Brown's collections from Australia, thereby misapplying the name to plants of *S. opacum.* It is interesting to note that he did not include Australia in the distribution given for *S. pterocaulon* in his 1852 account. Don's record of *S. pterocaulum* for Australia seems based solely on Dunal's protologue. Cheel being aware of Dunal's protologue and having access to Brown's specimen of *S. opacum* from Broad Sound (NSW) but not realizing the existence of two similar species, applied Dunal's name not only to plants of *S. nodiflorum* subsp. *nutans* but also to most plants of *S. opacum* he saw.

Baylis considered the plants Cheel referred to *S. pterocaulon* as being of *S. nodiflorum* on the basis of that author's illustration and recent collections from Sydney. While the plant illustrated in Plate 31 of Cheel's account is undoubtedly of *S. nodiflorum* subsp. *nutans,* at least three of the specimens he cited (Banks and Solander's, Brown's and Boorman's) are of *S. opacum.*

Dunal's misapplication of the name *S. oleraceum* to Australian plants is discussed under *S. nodiflorum.*

The stature of plants of *S. opacum* appears to be a very variable character though the low-growing or prostrate habit usually predominates. In some populations e.g. near Wilson's Peak in southeast Queensland, a range of habits from permanently erect to totally prostrate occurs. Constable (NSW 11098) records plants of this species as erect to 3 feet in populations at 3300 feet altitude near Wambool in New South Wales. In still other populations in southern Queensland plants have been observed to start erect but with age become procumbent.

The presence of a longitudinal purple stripe on the reverse of each petal of certain flowers appears directly under the control of a recessive gene. Plants have either all flowers on the one plant so coloured or all completely lacking the coloration, but never the two states intermixed. Both states can occur in the one

population but the frequency of coloured forms appears less than that of unmarked forms. Development of this coloration appears to be correlated with development of purple edging to the calyx and purple colorations on the stems.

Mature berries, though predominantly some shade of dull green may rarely be a mat purplish black in colour. Some collectors have noted this and it has also been personally observed in the field (*Henderson* 403, BRI) and in transplants grown under glasshouse conditions (*Henderson* 514, BRI). This could be a further expression of the recessive gene for purple coloration, evoked by a specific set of environmental circumstances. In the field instance, plants were growing through heaps of spilled superphosphate fertilizer, though in the glasshouse, chemical composition of the potting soil was not known. Intensity or exposure patterns of light seems a major factor in its occurrence since it developed only on surfaces not covered by the subtending calyx.

Only once has more than two sclerotic granules been observed in the mature fruit. In the population represented by *Henderson* 396, the fruit of one plant was found to have four granules in the usual position but here the fruit was larger than normal.

BIOLOGICAL AND CYTOLOGICAL OBSERVATIONS.—The chromosome complement of all plants examined cytologically was 72 (Table 1). This was determined from mitosis in root tips and tapetal tissue of anthers as well as meiosis in sporogenous tissue of anthers collected in the field or from plants grown under glasshouse conditions from field collections in Queensland.

In all cases observed, 36 daughter chromosomes were regularly formed following regular synapsis and bivalent formation during prophase stages of meiosis. In some instances, however, slight lagging at telophase II was evident and may account for the small percentage of sterile pollen seen in some specimens of this species.

The level of ploidy suggests an origin of *S. opacum* in some diploid progenitor, the species perhaps arising as a derivative of the supposedly native *S. nodiflorum* subsp. *nutans*. These two taxa have several characters in common though reciprocal cross-breeding experiments failed to produce hybrids. When plants of (6x) *S. opacum* were used as pollen parents, ovaries of plants of (2x) *S. nodiflorum* subsp. *nutans* developed to about half the usual size, were succulent and took on the purplish-black colour characteristic of the latter species but contained no trace of seed. When plants of this species were used as pollen parent, ovaries of *S. opacum* developed to normal size, remained opaque green when ripe and contained the numbers of seed characteristic of *S. opacum* but each of these seed comprised a collapsed testa without a functional embryo.

These fruit also contained the pair of sclerotic granules characteristic of *S. opacum*. The results of these breeding experiments indicate a strong genetic barrier to introgressive hybridization exists between these species in the field despite sympatric distribution in many localities.

**Solanum gracilius** Herter, Rev. Sudam. Bot. 7:226 (1943). Based on *S. gracile* Dun.

*S. gracile* Dun. in DC. Prod. 13,1:54 (1852); Baylis, Trans. Roy. Soc. N.Z. 85:379–385 (1958); non Sendt. in Mart. Fl. Bras. 10:13 (1846), nec Moric. hb. ex Dun. in DC. Prod. 13,1:238 (1852) pro syn. sub. *S. litocladum* incl. Type: Jard. de Montpellier, 29 Sep 1836, *A. DeCandolle* s.n. (lectotype G–DC, not seen; IDC 800–61.2063:III.7).

*S. gracile* Dun. var. *microphyllum* Dun. (l.c.). Type: in Central and South America (syntypes P, G–DC, not seen; IDC 800–61.2064:1, 2 & 3).

*S. gracile* Otto ex Cameron in Loud. Gard. Mag. 9:241 (1833) *nom. nud.*

*S. ottonis* Hylander in Upps. Univ. Ärsskr. 7:279 (1945); Willis, Hbk Pl. Vict. 2:552 (1972). Based on *S. gracile* Dun.

*S. gracile* Link ex A. Gray, Syn. Fl. N. Amer. 2, 1:228 (1886); Small, Man. SE. Fl. 1114 (1933); Radford, Ahles & Bell, Atlas Vasc. Fl. Carolinas, 192 (1965). Based on *S. gracile* hort. Berol.

Short lived perennial, bushy, much branched, erect or ascending, up to 1 (–1·5) m tall, often sprawling to ± 1 (–1·5) m across with branches long, ± weak and decumbent. Stems green or grey-green, rounded or somewhat angular, usually densely pubescent with erect or somewhat curved pallid eglandular hairs of unequal length. Leaves discolorous, deep-green to grey-green, almost whitish beneath; blades narrow ovate to elliptic, obtuse, contracted to the petiole, to ±16 cm long and 5 cm broad though usually much smaller, entire, sinuate or sometimes somewhat toothed, usually densely pubescent with strongly curved simple or rarely once-branched, pallid, eglandular hairs; petioles to ± 5 cm long, ± angled. Inflorescences (2–)4–7(–9)-flowered, occasionally leaf-opposed; peduncle simple occasionally bifurcate, rarely twice branched, erect or ascending and 1–2 cm long in flower, usually strongly deflexed from near its base and 2–2·5 cm long in fruit; rhachis condensed, internodes inconspicuous; pedicels decurved in flower, pendulous in fruit, 0·8–1·2 cm long. Flowers 1·2–2 cm diam. though corolla lobes becoming strongly reflexed at anthesis. Calyx in flower campanulate 1·5–3·5 mm long, in fruit flattened, appressed to the berry, 5–7 mm diam; lobes from semi-elliptic, obtuse, 0·8–1·5 mm long and 0·7–1(–1·5) mm broad in flower to somewhat deltoid, acute, 3–4 mm long and 2–3 mm broad in fruit, shortly pilose on the outer surface, hairs strongly curved. Corolla stellate,

white or occasionally tinged with purple, pale yellow-green towards the base of the tube inside, sometimes with a pair of purplish blotches towards the base of each lobe; lobes narrowly oblong to narrowly semi-elliptic acute, 4–8 mm long and (0·6–)2–4 mm broad, puberulous outside, hairs strongly curved. Stamens 3·5–5 mm long; filaments spreading hairy on the inner side; anthers (2·2–)2·5–3·5 mm long; pollen 24–26(–28) $\mu$ across. Style straight, spreadingly short hairy in the lower $\frac{2}{3}$, 5–6 mm long; stigma 0·3–0·4 mm diam, protruding 1–1·8 mm beyond the tips of the anthers. Mature fruit globose or slightly depressed (5–)7–9·5 mm diam, purplish black to black, dull, opaque, sclerotic granules usually absent, when present $< 0 \cdot 5$ mm across and at the apex of the fruit; seeds (10–)20–55, 1·4–1·8 mm long and $\pm$ 1·2 mm broad. Chromosome number: $2n(2x) = 24$. Infructescence—Plate 6 (B). Introduced.

QUEENSLAND.—MORETON DISTRICT: Clapham Junction, Brisbane, Jan 1966, Oct 1967, *Henderson* 128, 301 (BRI).

NEW SOUTH WALES.—NORTH COAST: Dorrigo, Mar 1949, *Fealy* NSW 71954 (NSW); Rocky Ck., SE of Dorrigo, Jan 1960, *Salasoo* 1815 (NSW). CENTRAL COAST: Botanic Gardens, Sydney, Mar 1915, *Boorman* NSW 99969 (NSW); Richmond, Dec 1921, *Carne* NSW 71959 (NSW); Glenorie, Sydney, Mar 1931, *Winter* NSW 71958 (NSW); Pennant Hills, Sydney, in 1934, *Frazer* NSW 71955 (NSW); Nepean R. gorge near Picton, Sep 1941, *Barnard* 12 (CANB); Parramatta District, Oct 1948, *anon.* NSW 71956 (NSW); Berry, Feb 1949, *Rodway* [NSW 71947] (NSW); Wahroonga, Sydney, Feb 1952, *Salasoo* 937 (NSW); Leumeah near Campbelltown, Dec 1952, *Evans* NSW 71946 (NSW); Carramar, Sydney, Jun 1953, *Francis* NSW 71960 (NSW); Castle Hill, Sydney, Jul 1954, *Hardman* NSW 71957 (NSW); Minto, Mar 1961, *Constable* NSW 71945 (NSW); Bardwell Park, Sydney, Nov 1961, *Chadwick* NSW 71992 (NSW); Liverpool, Apr 1963, *McBarron* 7960 (NSW); Cape Solander, southern head of Botany Bay, Jan 1965, *Constable* 5630 (NSW, ADW); Nepean R., Douglas Park, Sep 1965, *McBarron* 11054 (NSW), Oct 1965, *Constable* 6161, 6164 (NSW); Ingleburn, Feb 1968, *McBarron* 14881 (NSW). SOUTH COAST: Nowra, Jan 1935, *Rodway* [NSW 71949] (NSW); Broule Head, between Bateman Bay and Moruya, Dec 1948, *Rodway* [NSW 71948] (NSW); slopes of Mt. Dromedary, Central Tilba, Sep 1953, *Constable* NSW 71951 (NSW); Bodalla, Mar 1958, *Green* NSW 71950 (NSW); Montague I., Nov 1959, *Costin* NSW 71907, NSW 71908 (NSW); Currowan State Forest near Nelligen, Dec 1963, *Pullen* 3964 (NSW); Head of Moruya R., 15 miles W of Bodalla, May 1966, *Constable* 6897 (NSW). CENTRAL TABLELAND: Mt. Tomah, Jan 1966, *Ingram* (ADW), Feb 1966, *Ingram* NSW 99972 (NSW).

VICTORIA.—GIPPSLAND: Mitchell Rv. cliffs at "Colleea", $\frac{1}{2}$ mile N of Bairnsdale, Nov 1962, *Willis* (MEL); Mitchell R. near Paynesville, *Beauglehole* 37803 (ADW).

The species though native to South America was described principally from plants grown in the Montpellier gardens from seed from the Berlin gardens. In Australia it is obviously introduced probably originally to the Sydney Botanic Gardens and has become established to a moderate extent as a weed near habitations in temperate eastern coastal regions (Fig. 5). It appears not as common or prolific as *S. nodiflorum* or *S. nigrum*.

Baylis established that certain plants naturalized in New Zealand were conspecific with plants considered to be of *S. gracile* Otto by Jorgensen (cf. Jorgensen, 1928).

Some plants naturalized near Brisbane are considered to be conspecific with these New Zealand plants since plants grown from seed kindly provided by Professor Baylis (BRI 090652) agreed almost exactly with them morphologically. It is clear from the microfiches that they are also conspecific with plants which Dunal used as a basis of his description of *S. gracile.*

It appears that seed with the name *S. gracile* was distributed from the Berlin Botanic Gardens during the 1830's. In 1833, Cameron in a report on plants growing in the Birmingham Botanic Gardens in Loudon's Gardeners Magazine listed the name without a diagnosis, and attributed it without comment to Otto, probably because he was then the "Garten-direktor und Inspector Des Gartens" of Berlin. Otto appears not at any stage to have validly published the name. The first valid publication of this name for this species was by Dunal in 1852, for in his protologue he ascribed it to "Hort. Berol. e semin. in Hort. Monsp." and a note on one of his syntypes states *"Solanum gracile* h. ber. Fleurs blanches. Espèse nouvelle du Jard. de Berlin, euv. par lui sous ce nom. 3033/2 Aout 1832 Jard. de Genève." Dunal's name is however illegitimate being a later homonym of *S. gracile* Sendtner. Herter and Hylander independently provided a new name for this species based on Dunal's description but *S. gracilius* Herter (1943) has priority over *S. ottonis* (1945).

It seems that Link has at no stage validly published the name *S. gracile* as stated by A. Gray. As Link was Director of the Berlin Gardens in the 1830's it is presumed that citation of his name as author probably results in a similar manner to that of Otto's in the instance above. There is a Gray specimen from a cultivated plant (A–GH) labelled by him as "—e Link—"Solanum gracile" ", which seems to corroborate the above conclusion. Gray includes "Hort. Berol:Dunal l.c. 54 non Sendt." as further reference to the species dealt with by him and his description applies to Dunal's species also.

In each of these cases, typification depends on the type of *S. gracile* Dunal. The cultivated specimen from the Montpellier Gardens annotated by Dunal has been selected from the syntypes as lectotype of the species, since he clearly indicated that these plants formed the principal basis of his description.

At least one of the syntypes of *S. gracile* var. *microphyllum* Dun. (IDC 800–61.2064 : I.2) represents only a variation of *S. gracile* not considered worthy of formal recognition.

Stebbins and Paddock (1949) treat *S. gracile* in the sense of Gray (1886) as referring to *S. sarachoides* Sendt. In the light of the above specimen in the Gray Herbarium (A–GH) which is conspecific with Dunal's plant, and characters cited by Gray (viz. "flowers 11 mm across, white or bluish, with style exserted beyond the anthers and calyx somewhat appressed to the black berry"), it is obvious he was referring to *S. gracilius* and most certainly not to *S. sarachoides.*

Edmonds (1972) treated *S. gracilius* Herter as a taxonomic synonym of *S. sublobatum* Willd. ex Roemer & Schultes (Syst. Veg. 4:664, 1819) on the basis of specimen 4336 in the Willdenow herbarium and certain syntypes of *S. gracile* cited by Dunal. The microfiche of Willdenow's specimen (IDC 7440.298 : II.2) shows that the leaves are glabrous or sub-glabrous as Roemer and Schultes state for *S. sublobatum* but certainly not densely pubescent as are those on the lectotype of Dunal's species. In addition, anthers that can be measured are only 1·7–1·8 mm long, well outside the extremes of the range accepted for *S. gracilius.* Pollen size measurements should be made on both specimens and a detailed study of actual populations of living plants in South America undertaken to resolve this matter.

*S. subspatulatum* Sendt. (1846), treated by Edmonds as identical with *S. sublobatum,* was described by Sendtner as having fruiting peduncles erect and fruiting pedicels nodding and by Dunal as having glabrous stems and concolorous leaves all of which are discordant with *S. gracilius. S. isabellei* Dun. (1852), also treated by Edmonds as identical with *S. sublobatum,* was described by Dunal as having woody stems with an indumentum of brown-green, glandular hairs but this is difficult to corroborate from the microfiche of one of the syntypes (IDC 800–61.2074 : III.2). *S. gracilius* does not have glandular hairs.

Only one naturalized population of this species has been seen in the field. It was readily recognizable by an overall grey appearance with the distinctly discolorous, long narrow elliptic leaves often entire and tending to droop. The large flowers and dull black berries on deflexed peduncles are most characteristic. In some cultivated plants the calyx lobes though usually closely appressed to the berry showed a tendency to spread more or less horizontally when the berry is very ripe.

In the great majority of fruits examined on living plants including plants grown from Baylis's seed, and herbarium sheets, sclerotic granules were absent. However one or two granules were noted in some fruit on some specimens from New South Wales and according to Baylis New Zealand plants have from 0 to 4 grains per fruit. This is suggestive of some degree of hybridization possibly with *S. nodiflorum* subsp. *nutans.*

BIOLOGICAL AND CYTOLOGICAL OBSERVATION.—In all plants of undoubted *S. gracilius* collected in the field and cultivated in the glasshouse and examined cytologically, the somatic chromosome number was 24 (Table 1) which agrees with numbers recorded by Baylis (1958) and Vilmorin & Simonet (1928) for *S. gracile*.

Meiosis in young anthers and mitosis in seedling root tips were examined though not necessarily on the one plant. In the majority of preparations meiosis was normal but in some cells some lagging at anaphase I and anaphase II was noted though daughter cells of each tetrad invariably contained 12 chromosomes.

Gerasimenko & Reznikova (1968) record a sporophytic number of 72 for a species they list as "*S. gracile* hort." which agrees with counts in plants grown from seed from the Vilar Institute, Moscow, U.S.S.R. labelled "400 *Sol. gracile* Otto ex W. Baxt. yp 1966 VIII". These plants however appeared to be merely a form of *S. nigrum* L.

Progeny from seed collected beneath the first plants of *S. gracilius* recorded in Queensland, though resembling the parent somewhat, appeared more like a form of *S. nodiflorum*. They had shining black fruit borne in clusters of 3 or 4 in infructescences typical of subsp. *nutans*. Flowers though a little larger, also seemed of that species. On closer examination the fruit was found to be smaller (6 mm wide and 5 mm long) without any fully formed seed, the calyx spreading rather than reflexed and viable pollen varying from 18-27 $\mu$ across constituting only about 40% of all grains present. Since populations of *S. nodiflorum* subsp. *nutans* and subsp. *nodiflorum* were sympatric with these plants of *S. gracilius*, those raised were considered natural Fl hybrids. Their presence lends support to the supposition of dependancy by *S. gracilius* on some out-breeding for flower fertilization. These observations agree most strikingly with those reported by Baylis on artificially produced hybrids between these two species in New Zealand.

Fl individuals resulting from artificial hybridization of New Zealand plants of this species with plants of *S. douglasii* from seed from the U.S.S.R. were 16–18% pollen fertile. These individuals though robust set small numbers of fruit which contained little or no seed. Flowers though not exactly like either parent, were more like those of *S. douglasii* as was the form of the infructescences. The low percentage of viable pollen indicates a definite though incomplete barrier to introgressive hybridization between these two species.

**S. nitidibaccatum** Bitt. Fedde. Rep. 11:208 (1912); Curtis, Stud. Fl. Tas. 3:505 (1967); Beadle *et al.* Fl. Sydney Region 488 (1972); Willis, Hbk Fl. Vict. 2:551 (1972). Type: Chile, *Poeppig* s.n. (holotype, ?B†; ?isotypes, A, W, photo BRI).

MISAPPLIED NAMES:

? *S.villosum* auct. non (L.) Lam.; Black, Fl. S. Aust ed. 2(4) (rev. E. L. Robertson):746 (1957).

? *S. luteum* auct. non Mill.; Eichler, Suppl. Black Fl. S. Aust. ed. 2,271 (1965).

? *S. villosum* auct. non Mill.; Eichler, (loc. cit.).

Strictly annual, erect when up to ± 0·3 m tall or sprawling with the lower branches elongated, weakly trailing, to ± 0·6 m long. Stems pale green to somewhat straw-coloured or occasionally marked with purple, rounded occasionally ridged or almost narrowly winged by the decurrent leaves, ridges smooth, moderately to densely pubescent, hairs transparent, all ± spreading, of varying lengths intermixed (0·1–1·2 mm long) mostly glandular. Leaves pale green to dark green, somewhat discolorous; blades ovate to narrowly ovate to rhomboidal or trullate, acute or ± acuminate with the tip obtuse, truncate or abruptly contracted or shortly attenuate to the petiole, (1·5–)2·5–6(–9) cm long and (0·8–)1–3·5 cm broad, usually regularly toothed occasionally sinuate rarely entire, teeth where present obtuse not prominent, antrorsely directed, 4–7 on each margin, surfaces moderately pubescent with spreading, mostly glandular hairs; petioles 0·5–1·5 cm long, semi-circular or ± angular in cross-section. Inflorescences (3–)5–8(–12)–flowered; peduncle simple, spreading or ascending and up to ± 1 cm in flower, spreading or descending (0·4–)1–1·8 cm long in fruit; rhachis spreading or descending, internodes usually conspicuous the lowermost often much longer than the remainder and up to 1·5 cm long; pedicels decurved to erect in flower, decurved in fruit, up to 1·2 cm long. Flowers up to 1·4 cm diameter though corolla becoming strongly reflexed at anthesis. Calyx in flower infundibuliform and spreading to 0·5 cm, in fruit disproportionately enlarged the tube embracing the lower $\frac{1}{3}$–$\frac{1}{2}$ of the mature fruit, the lobes spreading to about 1·5 cm between tips; lobes narrowly semi-elliptic to ± narrowly triangular, acute, 1·25–2·5 mm long and 0·8–1·3 mm broad in flower, in fruit broadly triangular, up to 4 mm long and 5 mm broad, pilose on the outer surface, hairs spreading, glandular. Corolla rotate, white with small linear purplish markings towards the base of the tube, placed singly on each side of the mid-petaline veins; lobes deltoid to narrowly triangular, acute, 2·5–3·5 mm long and 2·75–3·5 mm wide, puberulous outside especially on the mid-petaline nerve and towards the tip. Stamens 4–4·5 mm long; filaments moderately to sparsely spreading hairy on the inner side; anthers 2–2·5 mm long; pollen (22–)23–27 $\mu$ across. Style straight, spreading short hairy in the lower $\frac{1}{2}$, 3·25–4 mm long: stigma from below the tips of the anthers to protruding slightly. Mature fruit globose or slightly depressed, olive green or somewhat dark brownish at maturity (or even jet black when over mature on ground beneath plant), with a contrasting lighter green or somewhat yellowish reticulum of veins visible through the cuticle, opaque or somewhat translucent, highly glossy, 7–7·5 mm long and 7·25–8·5 mm

broad, sclerotic granules 2, 0·5–0·8 mm across, placed at the apex of the fruit only; seeds 10–28, 1·7–2·3 mm long and 1·4–1·8 mm wide. Chromosome number: 2n (2x) = 24. Infructescence—Plate 6 (D). Introduced.

QUEENSLAND.—DARLING DOWNS DISTRICT: Glen Niven, Stanthorpe, Jan 1972, *Swann* (BRI); 28° 35′ S., 151° 58′ E., The Summit, ca 8 km NNE of Stanthorpe, Feb 1972, *Henderson & Parham* 1241 (BRI). MORETON DISTRICT: Wolffdene, near Beenleigh, Jul 1959, *Marshall* (BRI). CULTIVATED: Brisbane (seed ex Applethorpe (Darling Downs District) in 1964, *Johnson*), Mar 1968, *Henderson* 350 (BRI).

NEW SOUTH WALES.—CENTRAL COAST: Kogarah, Sydney, Feb 1898, *Camfield* NSW 72025 (NSW); Botanic Gardens, Sydney, Mar 1845, *Fry* NSW 71976 (NSW) [cult?]. CENTRAL TABLELANDS: Blayney District, Feb 1951, *Madsen* NSW 71990 (NSW). CENTRAL WESTERN SLOPES: Cowra, Jan 1960, *Green* NSW 71963 (NSW).

VICTORIA.—CENTRAL DISTRICT: Bannockburn, Mar 1924, *Hallebour* (MEL); Melbourne, Mar 1964, *Willis* (MEL, NSW); North Brighton, Melbourne, Mar 1965, *Willis* (MEL). GIPPSLAND: East Gippsland, at junction of Mt. Baldhead & Swift's Creek Roads, Feb 1971, *Beauglehole* 37084 (ADW).

SOUTH AUSTRALIA.—ADELAIDE PLAINS: River bed, Paradise, Apr 1952, *Dunstone* (ADW).

Curtis also records it as naturalized in Tasmania. In the absence of specimens her description seems to apply to this species.

The species is native to South America. In Australia it is clearly introduced probably independently on a number of occasions and persists principally as a weed of cultivation.

Though no type material (according to Edmonds, 1972, possibly only a photo at F now extant) has been examined, Australian plants agree with respect to critical characters with Bitter's protologue description. They are conspecific with plants grown from seed received under the name *S. nitidibaccatum* from the Vilar Institute, U.S.S.R. and with specimens labelled as *S. sarachoides* collected by Paddock in western U.S.A. (*Paddock* 416, 419, UC). They also agree with plants grown in South Australia from seed supplied by Heiser as *S. sarachoides* (ADW).

Roles's illustration of a British plant of *S. sarachoides* (no. 1057) in Clapham, Tutin & Warburg (1963), though somewhat stylized, is a good representation of Australian plants, especially in the descending nature of the fruiting peduncle, the obconical base of the flowering calyx and the spreading nature of the lobes of the fruiting calyx.

Some authors (e.g. Dandy, 1958; Gray, 1968; Edmonds, 1972) have recorded *S. nitidibaccatum* Bitt, as a synonym of *S. sarachoides* Sendt. (Sendtner in Mart. Fl. Bras. 10:18, 1846), while a number of others, mainly from North America, have either overlooked or ignored Bitter's name (e.g. Stebbins & Paddock, 1949; Fernald, 1950; Hitchcock *et al.,* 1959; Munz & Keck, 1959; Clapham *et al.,* 1962).

However, many others, mainly from Europe, have kept the names distinct and recorded both species from Europe (e.g. Hegi, 1927; van Oostroom *et al.,* 1966; Saarisalo-Taubert, 1967 and according to that author, Blom, 1936; Probst, 1949; Hylander, 1955; and Hansen, 1963).

It seems therefore that a detailed field study of living South American plants is required before the exact taxonomic position is known. After examination of a photograph of the lectotype chosen (by exclusion) by Bitter to typify *S. sarachoides* (*Sellow* [281], B†) on which anthers were 1·6–1·8 mm long, a photograph of a Chilean plant (*Philippi* [743], B†) determined as *S. nitidibaccatum* by Bitter and a probable duplicate (in A ex W) of the Poeppig specimen selected as holotype of *S. nitidibaccatum* by Bitter, I prefer to treat the species as distinct and include all Australian plants under *S. nitidibaccatum.* All herbarium material (including North American) and living plants studied are in better agreement with Bitter's species description than with Sendtner's and are conspecific with Poeppig's and Philippi's plants above. These photographs above are held at the Arnold Arboretum (A). The differences in handwriting on the labels suggest that automatically attributing numbers on the collection to the collector is not justified.

It should be pointed out that in his protologue Sendtner spelt the specific epithet "sarrachoides" above the description but as "sarachoides" in the text to the figures. The epithet is without doubt derived from the genus name *Saracha* Ruiz & Pavon so that Sendtner's spelling under the figures (i.e. only one r) is correct, that with the description being an orthographic error (ICBN Art. 73). The names misapplied to this species in Australian literature are discussed under *S. villosum.*

BIOLOGICAL AND CYTOLOGICAL OBSERVATIONS.—In all plants of this species examined cytologically, the somatic chromosome number was 24 (Table 1) which agrees with numbers previously recorded for *S. nitidibaccatum* by Ellison (1936), Westergaard (1948) and Gerasimenko and Reznikova (1968). It also agrees with that recorded for Paddock's plants under the name *S. sarachoides* by Stebbins and Paddock (1949). Observed meioses in pollen mother cells were regular or almost so, the small amount of lagging seen at anaphase I seeming to have little if any effect on viability of pollen which always measured greater than 98%.

**Solanum villosum** Mill. Gard. Dict. ed. 8: no. 2 (1768). Type: ex hb. Miller (lectotype BM, not seen, photo BRI).

*S. luteum* Mill. (loc. cit.) no. 3. Type: ex hb. Miller (lectotype BM, not seen, photo BRI).

*S. nigrum* L. var. *villosum* L. Sp. Pl. ed. 1:186 (1753). Based on *Solanum annuum hirsutius, baccis luteis*. Dill. Hort. Elth. 366, t. 274, f. 353 (1732).

*S. villosum* (L.) Lam. Tabl. Encycl. 2:18 (1794); Encycl. Meth. 4:289 (1797). Based on *S. nigrum* var. *villosum*.

*S. villosum* (L.) Willd. Enum. pl. 236 (1809). Based on *S. nigrum* var. *villosum*.

*S. nigrum* L. subsp. *villosum* (L.) Ehrh. Hann. Mag. 1780 (14): 218 (1780). Based on *S. nigrum* var. *villosum*.

*S. nigrum* L. subsp. *villosum* (L.) Pers. Syn. Pl. 1:224 (1805). Based on *S. nigrum* var. *villosum*.

*S. rubrum* Mill. (loc. cit.) no. 4; Benth. Fl. Aust. 4:446 (1869) non L. Syst. ed. 12, 2:173 (1767). Type: ex hb. Miller (lectotype BM, not seen, photo BRI).

MISAPPLIED NAME:

? *S. rubrum* auct. non L.; Nees ab Esenbeck in Pl. Preiss. 1:345 (1845).

Annual or short lived perennial, becoming bushy, much branched, erect, up to ± 0·5 m tall, with branches ascending. Stems green or ± pallid rarely deep reddish or marked with purple, rounded or somewhat angular, usually moderately to densely pubescent with spreading predominantly gland-tipped hairs or rarely with sparse strongly curved pallid eglandular hairs but then gland-tipped hairs present on seedlings. Leaves green or ± pallid or with veins and margins outlined with reddish purple, somewhat darker above; blades narrowly ovate to broadly ovate, obtuse or acuminate with the tip obtuse, abruptly contracted to the petiole, 1·5–5(–10) cm long and 0·7–2·5(–6·5) cm broad, entire, sinuate, irregularly or regularly toothed with obtuse antrorsely directed teeth, sub-glabrous to pubescent with hairs as on the stem; petioles 0·5–3(–4·5) cm long, ± angled. Inflorescences (2–)3–5(–8)-flowered; peduncle simple, ascending up to about 1·5 cm long in flower, to about 4 cm in fruit, 0·7–1·2 cm long. Flowers 0·8–1·5(–2) cm diam. though corolla lobes becoming strongly reflexed at anthesis. Calyx in flower campanulate to infundibuliform, 1·2–2 mm long, in fruit flattened to ± 8 mm across with lobes becoming moderately to strongly reflexed; lobes semi-elliptic to broadly semi-elliptic to bluntly deltoid, obtuse, 0·8–1 mm long and 0·5–0·8 mm broad in flower to ± 4·5 mm long and 2 mm broad in fruit, sparsely to moderately pubescent outside, hairs short, glandular or eglandular. Corolla rotate, white; lobes narrowly to broadly triangular, acute

or obtuse, 2·5–4·5(–5) mm long and 2–3·5 mm broad, puberulous outside, denser towards the upper margins. Stamens 2·5–5 mm long; filaments moderately to densely pilose on the inner surface with hairs spreading usually glandular, rarely glabrous; anthers (1·5–)1·8–2·2(–2·4) mm long; pollen (24–)26–33(–35) $\mu$ across. Style straight, spreading short hairy in the lower $\frac{2}{3}$, 3·5–4 mm long; stigma level with the tips of the anthers or protruding by up to 1 mm. Mature fruit ellipsoid somewhat longer than broad, 8·5–10 mm long and 8–9·5 mm wide, sclerotic granules absent; seeds 20–40, 1·7–2·3 mm long and 1·7–2·1 mm wide. Chromosome number: $2n(4x) = 48$. Infructescence—Plate 6(E) and 7(J). Introduced.

The only naturalized population examined occurred with the remnants of an old tobacco crop in an overgrown field in North Queensland. This population comprised largely senescent somewhat atypical plants. The bulk of Australian specimens examined have come from plants cultivated in Victoria, New South Wales and South Australia and grown in a glasshouse from seed collected from plants naturalized in Queensland and South Australia (Fig. 3).

QUEENSLAND.—COOK DISTRICT: ca 3 km S of Mareeba, Apr 1973, *Henderson* 1573 (BRI). CULTIVATED: Brisbane (seed ex Strathalbyn, S. Aust., 1962, *Symon*) Feb 1968, *Henderson* 354 (BRI); Brisbane (seed ex Walsh River, N. Qd, in 1966, *Cunningham*) Feb 1968, *Henderson* 351 (BRI).

NEW SOUTH WALES.—CULTIVATED: Sydney, Nov 1915, May 1916, *Cheel* [?] NSW 71953, NSW 112371 (NSW) (as *S. parviflora*); Sydney Botanic Garden, Apr 1916, *Boorman* NSW 71952 (NSW) as (*S. polyacanthos*).

VICTORIA.—CULTIVATED: Melbourne Botanic Gardens, Sep 1904, Mar 1906, *Baker,* ex hb. Baker (MEL).

SOUTH AUSTRALIA.—CULTIVATED: Waite Agric. Res. Institute (seed ex Strathalbyn, S. Aust.) Apr 1968, *Symon* (ADW).

Though the lectotype is from plants raised from seed, supposedly of West Indian origin, in the Chelsea Physic Garden, the exact origin of the species is unknown. In the light of Tandon and Rao's work (1964) *S. villosum* possibly has a Eurasian origin. In Australia the species is a rare introduction naturalized to a very minor extent and possibly not persistent. In North Queensland it occurred as a casual weed of crops of tobacco (*Nicotiana tabacum*).

The records of Nees (1845) and Turner (1898) suggest that this species may have been naturalized to some minor extent in Western Australia but there seems no corroborative evidence for its occurrence there.

Plants cultivated in Brisbane from seed of Australian origin are conspecific with specimens labelled variously as *S. luteum Mill.*, *S. villosum* Lam., *S. nigrum* var. *villosum* L. or *S. miniatum* Bernh. in GFW, and plants grown from seed labelled *S. luteum* from the Vilar Institute, Moscow, U.S.S.R. The herbarium material included five sheets from plants grown by Dr. Meindke-Wessely as *S. luteum* Mill. and the nomenclatural types of varietal names published under *S. luteum* in her paper (Wessely, 1960).

The wide range of variation noted in the comparatively small amount of Australian material is paralleled in the larger sample of European material examined and in the plants grown from European seed.

Constancy of characters of pollen, fruit and chromosomes even after hybridizations between seemingly widely differing forms, indicate that Australian material represents only one species exhibiting as much morphological variation as any other under study here.

From examination of photographs of the lectotypes of *S. luteum* Mill. and *S. villosum* Mill. held in BM, it is clear that these names are synonymous. Miller used colour of the fruit, together with minor differences in leaf shape and degree of hairyness to distinguish his species. Plants with orange-red fruits in lower infructescences and bright yellow fruits in upper infructescences occurred amongst plants raised from seed from U.S.S.R. (*Henderson* 556, BRI). Characters of leaves and indumentum are known to be quite variable in any one species.

Few authors since Miller's time considered these species identical. Since Stebbins and Paddock (1949) appear to be the first authors to treat the names as synonyms, I prefer to follow them in their choice of *S. villosum* for the species rather than use *S. luteum* as done by Wessely. Van Oostroom also considered the species identical and after extensive study of earlier literature took up *S. villosum* Mill. for this species in Fl. Neerlandica 4/2:159 (1966) on the basis of Stebbins and Paddock's paper (per. comm.). Since diagnostic characters visible in a photograph of the lectotype of *S. rubrum* Mill. held in BM, come within the range of variation of those of *S. villosum* that name is reduced to synonymy. Linnaeus's *S. nigrum* var. *villosum* and all the various combinations based on it are typified by the plate in Dillenius's Hortus Elthamus (1732). This is considered representative of the species Miller called *S. villosum* and the above names are therefore reduced to synonymy.

When Miller published *S. villosum* in his Dictionary, he was providing a name for plants actually known to him. He was not making a new combination in the rank of species of Linnaeus's varietal epithet *villosum*. The plants Linnaeus was referring to differed technically from Miller's in the colour of the fruit. Miller only therefore is treated as author of *S. villosum*.

Nees (1845) records *S. rubrum* L. var. from the Perth area of Western Australia. His description seems to refer to *S. villosum* Mill., but I have been unable to examine the specimen cited (hb. Preiss 1967).

Linnaeus, in his protologue to *S. rubrum* (Syst. nat. 2:173, 1767) described stems as sub-perennial and leaves as paired and entire. These characters hardly apply to *S. villosum* of Miller, plants of which Linnaeus included under *S. nigrum* var. *villosum*. No type material of *S. rubrum* L. has been examined, though a specimen in the Linnean herbarium (IDC 177–5. 138:I. 3,4 (248·6)), possibly of this species (Savage, 1945), in no way resembles plants of *S. villosum* Mill. Nees seems therefore to have misapplied the Linnean name to the West Australian plant.

The record of *S. villosum* Lam. for South Australia in Robertson's revised edition of Black's Flora is almost certainly based on a specimen of *S. nitidibaccatum* collected by Dunstone and determined by Robertson as *S. villosum* (ADW). Eichler, in his Supplement to the second edition of Black's Flora, changed the entry under *S. villosum* Lam. to "*S. luteum* Mill. ( *S. villosum* Mill.)" solely on the basis of Wessely's paper in 1960 (pers. comm.).

The north Queensland provenance resembles *S. nigrum* in many characters, especially in the racemiform arrangement of the fruit, the lack of spreading gland tipped hairs in the indumentum of adult plants and the size of anthers and pollen making dried specimens difficult to identify positively. The deltoid corolla lobes shorter than the tube, the stiffly ascending peduncle with sharply deflexed pedicels, the strongly recurved calyx behind the longitudinally ovoid fruit and the somewhat coarser toothing of the leaf serve to distinguish specimens of *S. villosum*.

The variation observed in this species in Australia suggests a subdivision into subspecies or varietal categories as proposed by Wessely may be justified. However it seems preferable for the present to refrain from formal sub-division until much more material of the northern Australian plants can be studied as none of these exactly matches material of any of the intraspecific categories proposed by Wessely.

BIOLOGICAL AND CYTOLOGICAL OBSERVATIONS.—In all plants of this species examined cytologically, the somatic chromosome number was 48 (Table 1) which agrees with numbers previously recorded for *S. villosum* (or *S. luteum*) by numerous authors (e.g. Jorgensen, 1928; Stebbins & Paddock, 1949; Tandon & Rao, 1966; Gerasimenko & Reznikova, 1968; and Venkateswarlu & Rao, 1969). Chromosomes were observed at meiosis in pollen mother cells and mitosis in root tips of seedlings though not necessarily from the same plant. In

all plants of Australian origin meiosis was normal with 24 bivalents occurring regularly. Separation was even and daughter cells with 24 chromosomes were invariably produced. Some evidence of chromosome lagging and mis-division during meiosis was noted in progeny of seed from U.S.S.R. though in all plants from this source, estimated pollen viability was at least 90%.

However, plants raised from the seed from north Queensland, though tetraploid with normal meioses, had pollen viability ranging to as low as 65% and as previously noted displayed certain characteristics typical of *S. nigrum*. This suggests that introgressive hybridization with *S. nigrum* known to be sympatric in that area, may have occurred. Such a cross has been shown possible at least experimentally, despite the differences in ploidy levels (4x and 6x), by Jorgensen (1928) and Tandon & Rao (1966).

Plants typical of *S. villosum* grown from seed (labelled "408 *S. luteum* Mill. yp 1967 VIII") from U.S.S.R. reciprocally hybridized with plants grown from seed originally from north Queensland produced Fl plants resembling more the pollen parent of each cross, though pollen remained 95–100% viable. In each case colour of fruit on Fl progeny was orange-red though that of the parent from seed from U.S.S.R. was bright yellow. Ovaries of European plants fertilized with pollen from north Queensland plants developed normally and contained normal numbers of well filled seed. Plants from this seed (*Henderson* 484, BRI) were however more vigorous than either parent. However, ovaries of north Queensland plants fertilized with pollen from European plants did not reach normal size and the number of seed was greatly reduced, though still fully fertile. The resultant Fl individuals (*Henderson* 515, BRI) were fully fertile though in stature were intermediate between the parents. This evidence tends to support some intraspecific subdivision.

**Solanum furcatum** Dun. in Poir. Encycl. meth. Suppl. 3:750 (1814) ("1813"); Curtis, Stud. Fl. Tas. 3:504 (1967). Type: Peru, *Dombey* s.n., ex hb. Dombey (holotype P, not seen).

MISAPPLIED NAME:

*S. douglasii* auct. non Dun.; Willis, Hbk Fl. Vict. 2:551 (1972).

Perennial, becoming somewhat shrubby, sprawling to ± 2 m across. Stems green or partially marked with purple, slender, straggling, scrambling over other vegetation, angular or narrowly winged, the ridges with or without short erect soft prickle hairs or pricklets ("teeth" of other authors), sub-glabrous to moderately pilose with strongly curved eglandular hairs. Leaves green or marked with purple, somewhat discolorous; blades narrow elliptic to narrowly ovate, acute, obtuse or with the tip almost semi-circular, abruptly contracted or

gradually attenuate to the petiole, up to 10 cm long and 3·5 cm broad, entire, sinuate or irregularly shallowly lobed, the lobes spreading obtuse or almost semi-circular, up to 7 on each margin, sub-glabrous to moderately pilose on each surface with strongly curved, eglandular hairs; petioles 0·7–2·5 cm long, ± narrowly winged. Inflorescences 4–14-flowered, occasionally leaf opposed; peduncles simple, bifurcate or rarely twice branched, erect or ascending and up to ± 2·5 cm long in flower, horizontally spreading or deflexed and up to ± 3 cm long in fruit; rhachis spreading, internodes usually conspicuous; pedicels decurved to stiffly erect and up to 0·8 cm long in flower, decurved or pendulous and up to 1·2 cm long in fruit. Flowers 12–20 mm diam. though corolla lobes becoming strongly reflexed at anthesis. Calyx in flower campanulate, ± 3 mm long, in fruit flattened and appressed to the berry, up to ± 7 mm diam.; lobes semi-elliptic to broadly triangular, obtuse, 1–1·5 mm long and ± 1 mm wide in flower enlarging to 1·5–2·5 mm long and 1·3–2 mm broad in fruit, sparsely to moderately pilose outside, hairs strongly curved, eglandular. Corolla stellate, white or variously tinged with purple especially outside; lobes narrowly ovate or triangular to ovate, acute, 4–6 mm long and 3–3·5 mm wide, moderately to densely pilose outside especially towards the tip, hairs strongly curved. Stamens 4–6 mm long; filaments broad, spreading hairy on the inner side; anthers 2·3–3·3(–3·6) mm long; pollen 30–33(–37) $\mu$ across. Style straight, spreading hairy in the lower $\frac{1}{2}$–$\frac{2}{3}$, up to ± 7·5 mm long; stigma 0·4 mm across, protruding 2–3 mm beyond the tips of the anthers. Mature fruit globose, black, dull, 6–9 mm across, sclerotic granules several (up to ± 12) probably dispersed in pairs throughout the fruit, 0·5–1·2 mm across; seeds 30–40, ± 2 mm long and 1·5 mm wide. Chromosome number: 2n(6x) = 72 (Stebbins & Paddock, 1949). Introduced.

VICTORIA.—CENTRAL DISTRICT: McCrae, Mornington Peninsula, Feb 1963, *Willis* (MEL); St. Leonard's, Bellarine Peninsula, Oct 1963, *Willis* (MEL).

These specimens, annotated by Baylis as possibly of *S. douglasii*, form the basis of Willis's record of that species from Victoria.

*S. furcatum* is native to South America. In Australia it is definitely known only from this one small near-coastal area in southern Victoria though Curtis reports it as a rare introduction in northern Tasmania (Fig. 5). In the absence of specimens from that State, her description certainly seems to apply to this species. There is however no evidence to suggest that it has persisted in any of these localities in Australia.

Though no type material has been examined the Australian material is not discordant in any way with Dunal's protologue description which is unfortunately somewhat brief. It is conspecific with Paddock's specimen labelled by him as

*S. furcatum,* from Westport, California, U.S.A. (*Paddock* 167, UC). Though no living material has been studied, application of Dunal's name to Australian specimens is considered justified.

**Solanum retroflexum** Dun., DC. Prod 13,1:50 (1852). Type: In promont. Bonae Spei, in 1838, *Drege* 7864 a & b (syntypes G-DC, not seen; IDC 800-61. 2062:II. 1 & 2).

Apparently annual, at first erect but lateral branches becoming long and decumbent, the plant appearing bushy, up to ± 0·5 m tall and 1 m across. Stems green, angular or narrowly winged, the ridges smooth, sparsely pilose, hairs eglandular, somewhat spreading on young stems, strongly curved on adult stems. Leaves green conspicuously discolorous; blades ovate to elliptic, obtuse, contracted abruptly to the petiole, up to ± 8 cm long and 5·5 wide, regularly and deeply lobed, lobes obliquely triangular, acute obtuse or even semi-circular, spreading or ± antrorsely directed, up to 5 on each margin, sparsely to moderately pubescent, hairs strongly curved eglandular; petiole up to ± 4 cm long, ± narrowly winged. Inflorescences 4–7-flowered; peduncle simple, erect or ascending, 0·4–1·4 cm long in flower, up to ± 2·5 cm in fruit; rhachis horizontally spreading or decurved, condensed, all but the lower 1 (or 2) internodes usually inconspicuous; pedicels decurved, 4–6 mm long in flower, pendulous up to 12 mm long in fruit. Flowers commonly up to ± 1·2 (rarely to 1·4) cm diam. though corolla lobes becoming reflexed after anthesis. Calyx in flower campanulate, 2–2·5 mm long, in fruit flattened with lobes from ± spreading-recurved to strongly reflexed, about 7 mm across, lobes semi-elliptic to narrowly triangular obtuse or acute, up to ± 1·5 mm long and 0·7 mm wide in flower, up to ± 3 mm long and 1·5 mm wide in fruit, sparsely pilose outside with strongly curved eglandular hairs. Corolla stellate, white, creamy yellow or occasionally with a longitudinal purple stripe in the centre of the outside of each lobe; lobes narrowly triangular to oblong or narrowly ovate, acute, 2·5–4·5 mm long and 1·3–2·5 mm broad, ± shortly pilose outside. Stamens ± 2·5 mm long; filaments broad, spreading hairy on the inner side; anthers 1·3–1·8(–2) mm long; pollen (24–)25–28 $\mu$ across. Style straight spreading hairy in the lower $\frac{1}{3}$, 1·9–2·2 mm long; stigma ± 0·2 mm across, from below the tips of the anthers to protruding by up to 0·5 mm. Mature fruit globose or slightly depressed, jet black, dull, (3–)5–8 mm long and (3–)6–9 mm wide with sclerotic granules 2–4(or possibly absent), 0·1–0·5 mm across, placed at the apex or also equatorially; seed (5–)12–35, ± 1·8 mm long and 1·3–1·6 mm wide. Chromosome number: 2n(4x) = 48. Infructescence—Plate 6(C). Introduced.

SOUTH AUSTRALIA.—EYRE PENINSULA: "Pillie Waterhole", Hundred of Flinders, south-eastern tip of Eyre Peninsula, Nov 1966, *Alcock* 1268 (AD), Apr 1968, *Alcock* 2099 (ADW).

Dunal described the species from specimens from South Africa and Arabia. In Australia it is known naturalized only in one locality in South Australia (Fig. 3). However plants grown from seed from this locality in the field at Brisbane have indicated that the species is able to persist unassisted in hot, dry or little-watered situations in Queensland. It is probably therefore a recent introduction to this continent.

Of the two syntypes in the DeCandolle Prodromus Herbarium, the specimen determined as *S. retroflexum β augustifolium* (*Drege* 7864b) by Dunal appears conspecific with the Australian plant. However in the absence of a thorough understanding of the species over the whole of its range, it seems preferable at this stage to refrain from selecting a lectotype.

Sufficient fruit of this species has not been available to determine the exact position with regard to sites of occurrence of sclerotic granules. As noted by Baylis with other species, where these structures are extremely small (i.e. $<0 \cdot 1$ mm) their presence may be easily overlooked.

Chromosome numbers (Table 1) were established from meioses in pollen mother cells from plants grown in Brisbane from seed from South Australia.

**Solanum scabrum** Mill. Gard. Dict. ed. 8: no. 6 (1768); non Vahl, Eclo. 1:22 (1797); nec Lam. Encycl. Meth. 4:291 no. 19 (1797); nec Ruiz & Pav. Fl. Peru 2:39, t.175, f.*a* (1799); nec Jacq. Pl. Rar. hort. caes. Schoen. 3:45, t.333 (ca. 1803); nec Zuccag. Cent. 5:50 (1806); nec Dun. Sol. p. 194 (1813). Type: ex hb. Miller (lectotype BM, not seen, photo BRI).

*S. melanocerasum* All. Auct. Syn. 12(1773); non Willd. Enum. Pl. 237 (1809). Based on *Solanum Guineense, fructu magno, instar Cerasi, negerrimo, umbellato* Dill. Hort. Elth. 366 ("336") (1732).

*S. nigrum* L. var. *guineense* L. Sp. Pl. 186 (1753). Based on *Solanum Guineense . . . umbellato.*

*S. guineense* (L.) Mill. Gard. Dict. ed. 8: no. 7 (1768); non L. Sp. Pl. 184 (1753). Based on *S. nigrum* var. *guineense.*

*S. guineense* (L.) Lam. Tabl. Encycl. 2:18, no. 2339 (1794); Dun. in DC. Prod. 13,1:49 (1852). Based on *S. nigrum* var. *guineense.*

*S. guineense* (L.) Willd. Enum. Pl. 237 (1809). Based on *S. nigrum* var. *guineense.*

*S. intrusum* Soria, Baileya 7:33 (1959). Based on *Solanum Guineense . . . umbellato.*

Short lived perennial though grown as an annual, shrubby, erect or ascending, up to $\pm$ 1 m tall. Stems deep green, smooth, angled or narrowly winged by the decurrent leaves, the ridges smooth or with short soft pricklets, usually glabrous

except when very young, hairs where present strongly curved, eglandular. Leaves deep green; blades ovate to broadly elliptic, acute, shortly cuneate, abruptly contracted or almost truncate at the base, up to 15 cm long and 8 cm broad, entire or occasionally sinuate, glabrous on both surfaces or glabrescent with few strongly curved eglandular hairs on younger leaves; petioles 1–7 cm long, narrowly winged. Inflorescences 5–9(–15)-flowered; peduncle simple or rarely once forked, ascending, 1–2·2(–4) cm long in flower, in fruit ascending horizontally spreading or somewhat decurved from the weight of the fruit, up to ± 5 cm long; rhachis condensed, internodes inconspicuous; pedicels from erect to decurved in flower, divaricate, from erect to pendulous in fruit when 1–1·4 cm long. Flowers 8–12 mm diam. Calyx in flower campanulate, 2·5–3 mm long, in fruit somewhat enlarged with the lobes strongly reflexed; lobes unequal, semi-elliptic to semi-circular, acute, obtuse or rotund, 1·5–2 mm long and about 1·2 mm broad in flower, up to 3·5 mm long and 2·5 mm wide in fruit, glabrous. Corolla stellate, white; lobes ovate, narrowly ovate to narrowly triangular, acute, 3–4 mm long and 2·2–2·7 mm broad, puberous outside towards the tip and upper margins. Stamens 3–4 mm long; filaments densely spreading hairy on the inner side, flattened, the base ± 1 mm broad; anthers 2·5–3 mm long; pollen (24–)25–28(–30) $\mu$ across. Style straight, stout, spreading hairy on the lower ½, up to 2·5 mm long; stigma ± 0·4 mm across, level with the tips of the anthers or enclosed within them. Mature fruit globose or slightly depressed, purplish black, opaque, highly glossy, up to about 14 mm long and (10–)12–16 mm wide; sclerotic granules absent; seeds up to ± 80, 2–2·8 mm long and 1·6–1·8 mm wide. Chromosome number: 2n(6x) = 72. Introduced but not naturalized.

QUEENSLAND.—CULTIVATED: Brisbane garden, Feb 1920, *Coleman* (BRI); Botanic Gardens, Brisbane (seed ex Sunshine Floral Farm, northern N.S.W.) May 1958, *Trapnell* (BRI).

VICTORIA.—CULTIVATED: Botanic Gardens, Melbourne, Mar 1892, *St. John* (MEL).

SOUTH AUSTRALIA.—CULTIVATED: Waite Agric. Res. Institute, Adelaide (seed ex Vilar Institute, U.S.S.R.) Apr 1968, *Symon* (BRI) (seed ex Montreal Botanic Gardens) Apr 1968, *Symon* (BRI).

The species is described as a native to Guinea but according to Heine (1960) is most certainly not native to any part of Africa. Its actual origin is unknown. In Australia it is known only in cultivation, seed having been sold to a minor extent some years ago in the garden trade as Huckleberry or Garden Huckleberry. The above description is based on the herbarium material cited, and Cheel's plate 32 (Cheel, 1917).

Since most authors consider it belongs to a distinct species, the correct name at species level for the plant Linnaeus called *S. nigrum* var. *guineense* has been the subject of study and discussion by a number of authors (e.g. see synonomy above and Polgár, 1940; Heine, 1960 and Heiser, 1969). It is now generally

agreed that *S. melanocerasum* Allioni is the oldest nomenclatural synonym in the rank of species for this plant (Dandy, 1970).

Examination of photographs of plants in Miller's herbarium (BM) brought under attention the plant labelled *S. scabrum*. Through the courtesy of Dr. W. T. Stearn the anther lengths and pollen grain sizes on this specimen were measured. The anthers are "ca 2·2 mm" and the pollen grains are "$25 \cdot 8\ \mu \times 21 \cdot 5\ \mu$ — $32 \cdot 2\ \mu \times 21 \cdot 5\ \mu$" which indicates that the plant was probably hexaploid. In the protologue to *S. scabrum* Miller presented a diagnosis which agrees exactly with this specimen. By stating "foliis integerrimis" he excludes the plate in Dillenius's Hortus Elthamus (cited in the protologue) from consideration in typification. The specimen therefore is selected as lectotype of the species (Plate 5).

Besides general agreement in measurements of anthers and pollen grains, this specimen can be matched in other details of floral and vegetative characters with luxuriant specimens of *S. melanocerasum* All. *S. scabrum* Mill. and *S. melanocerasum* All. are therefore considered synonymous. Miller's name, dating from 1768, has priority over Allioni's and the homonyms cited above and is therefore the correct name for the species.

Miller's specimen is in flower only so that the reference to fruiting characteristics in his protologue (in discord with the plants previously known as *S. melanocerasum* All.) must therefore have been taken from some other source (possibly Dillenius). As such there is no evidence that Miller observed them on the plant from which the lectotype was gathered.

Chromosome number in the species was determined from meioses in pollen mother cells in plants from seed from the Sunshine Floral Farm in northern New South Wales. Its origin is not definitely known, but it is thought to have come via a seed merchant in U.S.A. (Trapnell, pers. comm.).

**Solanum douglasii** Dun. in DC. Prod. 13,1:48(1852). Type: Nova California, in 1839, *Douglas* s.n. (holotype G-DC, not seen; IDC 800-61. 2061:III.8).

Perennial, somewhat shrubby, erect or ascending, up to ± 1 m tall. Stems green or variously marked with purple, slender, angular or narrowly winged, the ridges smooth or with evenly spaced short erect soft prickle hairs or pricklets, sub-glabrous to moderately pubescent with strongly curved eglandular hairs. Leaves green or marked with purple, somewhat discolorous, when young emitting a strong foetid odour when bruised; blades ovate, narrowly ovate to narrowly elliptic, acute, abruptly contracted or attenuate to the petiole, 3–10(–17) cm long and 1·3–5(–7·5) cm broad, regularly or irregularly lobed, rarely entire, lobes where present acute, low, antrorsely directed, up to 10 on each margin, moderately to densely pubescent on each surface with strongly curved eglandular

hairs; petioles 1–3(–7) cm long, ± narrowly winged. Inflorescences (3–)6–14-flowered, internodal or leaf-opposed; peduncles simple or possibly rarely once branched, erect or ascending up to ± 3 cm long in flower, to ± 4·5 cm in fruit; rhachis spreading or decurved, internodes usually conspicuous; pedicels decurved to erect in flower, pendulous or decurved in fruit, up to ± 1·5 cm long. Flowers 12–15(–20) mm diam. though corolla lobes becoming strongly reflexed at anthesis. Calyx in flower campanulate, ± 3 mm long, in fruit flattened and appressed to the berry, up to ± 8 mm diam.; lobes semi-elliptic to broadly triangular, obtuse, 0·8–1·5 mm long and 0·8–1 mm wide in flower, 1·25–4 mm long and 1·5–1·75 mm wide in fruit, moderately pilose outside, hairs strongly curved, eglandular. Corolla stellate, white or variously tinged with violet or wholly violet; lobes narrowly ovate to narrowly triangular, acute, 4·5–5·5 mm long and 2·5–4 mm wide, moderately to densely pilose outside especially towards the margins and tip, hairs strongly curved. Stamens 4·5–5·5 mm long; filaments broad, spreading hairy on the inner side; anthers 3·25–4·25 mm long; pollen 21–23(–27) $\mu$ across. Style straight, spreading short hairy in the lower $\frac{2}{3}$, up to ± 8 mm long; stigma 0·2 mm across, protruding 1·7–2·25 mm beyond the tips of the anthers. Mature fruit globose, black, dull, 6–8 mm across, sclerotic granules 0–8 (position undetermined), less than 0·5 mm across; seeds ± 50, 1·5–1·8 mm long and 1·2–1·5 mm wide. Chromosome number: $2n(2x) = 24$. Introduced but not naturalized.

The species was described by Dunal from specimen(s) collected in California, U.S.A. but appears to be native to Central America and northern regions of South America. In Australia it is known only in cultivation. The above description is based on plants cultivated in Brisbane from seed from Moscow, U.S.S.R. labelled *S. douglasii,* on specimens collected in California and labelled *S. douglasii* by Paddock (UC) and specimens of plants grown by Baylis from seed from Carpentaria, California (MEL). A number of specimens of plants grown at the Waite Agricultural Research Institute, South Australia have also been examined (ADW).

Examination of the microfiche of Douglas's plant supports the application of Dunal's name to this material.

Edmonds (1972) considered *S. nigrescens* Mart. & Gal. the correct name for this species. According to Polgár (1940), Bitter examined type material of that species in the Vienna State Museum (W) and recorded that the fruits on the specimen contained about eleven sclerotic granules and the leaves were completely entire. These characteristics agree more with *S. furcatum* than with *S. douglasii.*

Chromosome numbers (Table 1) were established from meioses in pollen mother cells from plants grown in Brisbane from the seed from Moscow, U.S.S.R. The results of artificial hybridization using plants of this species as one parent are discussed under *S. gracilius.*

# INDEX

## SPECIES NAMES

## BIBLIOGRAPHY

ALEXANDER, M. P. (1969). Differential staining of Aborted and non-aborted Pollen. *Stain Tech.* 44:117-122.

BAILEY, F. M. (1881). A Few Remarks on our Naturalized Solanums. *Trans. Phil. Soc. Qd* 3:1-4.

BAILEY, F. M. (1883). Syn. Qd Fl. 342.

BARANOV, A. I. (1967). Wild Vegetables of the Chinese in Manchuria. *Econ. Bot.* 21,2:140-155.

BAYLIS, G. T. S. (1954). Chromosome number and Distribution of *Solanum aviculare* Forst. and *S. laciniatum* Ait. *Trans. Roy. Soc. N.Z.* 82:639-643.

BAYLIS, G. T. S. (1958). A Cytogenetical Study of New Zealand forms of *Solanum nigrum* L., *S. nodiflorum* Jacq. and *S. gracile* Otto. *Trans. Roy. Soc. N.Z.* 85:379-385, pl. 25.

BENTHAM, G. (1869). Solanaceae *in* Flora Australiensis 4:442-470.

BITTER, G. (1911). Solana nova vel minus cognita. I. *Fedde. Rep.* 10:529-565.

CHEEL, E. (1917). Notes on the "Common Nightshade" (*Solanum nigrum* L.) and some closely related forms and species that have been confused with it. *Proc. Linn. Soc. N.S.W.* 42:583-602, Pl. 30-33.

CHENNAVEERAIAH, M. S., & PATIL, S. R. (1968). Some Studies in the *Solanum nigrum* L. Complex. *Gen. Iber.* 20:23-36.

CLAPHAM, A. R., TUTIN, T. G., & WARBURG, E. F. (1963). Fl. Brit. Isles Illustr. pt. 3:13.

CURTIS, W. M. (1967). The Students Flora of Tasmania pt. 3:505.

DANDY, J. E. (1958). List of British Vascular Plants. London: Trustees of the British Museum.

DANDY, J. E. (1970). Annotated List of the New Names Published in Allioni's Auctarium ad Synopsim Stirpium Horti Reg. Taurinensis. *Taxon* 19:617-626.

DUNAL, M. F. (1813). Hist. Sol. p. 153.

DUNAL, M. F. (1852). Solanaceae *in* De Candolle Prod. 13, pt. 1:1-690.

EDMONDS, J. M. in STEARN, W. T. (1971). Taxonomic and Nomenclatural Notes on Jamaican Gamopetalous Plants. *J. Arn. Arb.* 52:634-635.

EDMONDS, J. M. (1972). A Synopsis of the Taxonomy of *Solanum* sect. *Solanum* [Maurella] in South America. *Kew Bull.* 27 (1):95-114.

EDWARDSON, J. R. (1956). Cytoplasmic male-sterility. *Bot. Rev.* 22:696-738.

ELLISON, W. (1936). Synapsis and Sterility in a *Solanum* Hybrid. *J. Gen.* 32:473.

ERDTMAN, G. (1952). Pollen Morphology and Plant Taxonomy—Angiosperms. Stockholm: Almqvist & Wiksell. Waltham, U.S.A.: The Chronica Botanica Co.

EVERIST, S. L. (1973). Poisonous Plants of Australia. Sydney: Angus & Robertson (Publisher) Ltd. (in press).

FERNALD, M. L. (1950). Gray's Manual of Botany. ed. 8. New York: American Book Co.

FORSTER, G. (1786). Fl. Ins. Aust. Prod. p. 89.

FRANCIS, F. J. & HARBORNE, J. B. (1966). Anthocyanins of the Garden Huckleberry, *Solanum guineense*. *J. Food Sci.* 31:524-528.

GERARD, J. (1597). The Herball, or Generall Historie of Plants. London: J. Norton.

GERASIMENKO, I. I. & REZNIKOVA, S. A. (1968), *in* Index to Plant Chromosome numbers for 1968 (1970). *Reg. Veg.* 68:74.

GRAY, J. (1968). The Taxonomy of the Morella Section of the Genus *Solanum* within South America. Unpub. Ph.D. Thesis, University of Birmingham, England.

HAUSER, E. J. & MORRISON, J. A. (1964). The Cytochemical Reduction of Nitro Blue Tetrazolium as an Index of Pollen Viability. *Amer. J. Bot.* 51(7):748-752.

HEGI, G. (1927). Illus. Fl. von Mittel-Europa. 5(4):2586.

HEINE, H. (1960). Notes on *Solanum*. *Kew Bull.* 14:245.

HEISER, C. B. JR. (1955). The *Solanum nigrum* complex in Costa Rica. Cieba 4:293-299.

HEISER, C. B. JR. (1963). Estudio Biosistematico de *Solanum* (Morella), en el Ecuador. *Cien. y. Nat.* 6(2):50-58.

HEISER, C. B. JR. (1969). Nightshades, The Paradoxical Plants. San Francisco: W. H. Freeman & Co.

HEISER, C. B. JR., SORIA, J. & BURTON, D. L. (1965). A Numerical Taxonomic Study of *Solanum* species and Hybrids. *Amer. Nat.* 99, no. 909:471-488.

HEPPER, F. N. (1968). A Standard Citation of Microfiches. *Taxon* 17:604.

HITCHCOCK, C. L., CRONQUIST, A., OWNBEY, M. & THOMPSON, J. W. (1959). Vascular Plants of the Pacific Northwest 4. Seattle: University of Washington Press.

JORGENSEN, C. A. (1928). The Experimental Formation of Heteroploid Plants in the genus *Solanum*. *J. Gen.* 19:133-211.

KAUL, C. L. & SINGH, S. P. (1969). Validity of Stain Tests in determining Pollen Viability of some Papilionaceous Plants. *Ind. J. Agric. Sci.* 39(2):1050-1056.

LEICHHARDT, L. (1847). Journal of an Overland Expedition in Australia from Moreton Bay to Port Essington during the years 1844-1845. London: T. & W. Boone.

MCBARRON, E. J. (1955). An Enumeration of Plants in the Albury, Holbrook and Tumbarumba Districts of New South Wales. *Contr. N.S.W. Nat. Herb.* 2:89-247.

NAKAMURA, M. (1935). Preliminary note on the polyploidy in *Solanum nigrum* L. *J. Soc. Trop. Agric.* 7:255-257.

NAKAMURA, M. (1937). Cytological Studies in the Genus *Solanum* I. Autopolyploidy of *Solanum nigrum* L. *Cytologia, Fujii Jub. Vol.*: 57-68.

ODASHIMA, K. (1936). Plantarum Formosanarum species novae determinatae II. *J. Soc. Trop. Agric.* 8:54-62.

PADDOCK, E. F. (1941). Natural and Experimental Polyploidy in *Solanum douglasii* Dun. and its relatives. *Amer. J. Bot.* 28:727.

PEGG, K. G. & MOFFETT, M. L. (1971). Host range of the ginger strain of *Pseudomonas solanacearum* in Queensland. *Aust. J. Exp. Agric. Anim. Husb.* 11:696-698.

POLGÁR, S. (1940). *Solanum dillenianum*. *Meddel. Göte. Bot. Träd.* 13:281-288.

RADFORD, A. E., AHLES, H. E., & BELL, C. R. (1965). Atlas of the Vascular Flora of the Carolinas. *Univ. N. Carolina Tech. Bull.* 165:192.

RAI, U. K. (1959). A Forty Chromosome Variant in *Solanum nigrum* L. *Nature,* 4698:1587.

ROE, K. E. (1971). Terminology of Hairs in the Genus *Solanum*. *Taxon* 20(4):501-508.

SAARISALO-TAUBERT, A. (1967). Adventive *Solanum* species of the group Morella in Eastern Fennoscandia. *Annal. Bot. Fenn.* 4(1):87-94.

ST. JOHN, H. & HOSAKA, E. Y. (1932). Weeds of the Pineapple Fields of the Hawaiian Islands. *Univ. Hawaii Res. Pub. no.* 6:136-137.

SALAMAN, R. N. (1909). Male Sterility in Potatoes, a dominant Mendelian character; with remarks on the Shape of the Pollen in Wild and Domesticated Varieties. *J. Linn. Soc. Bot.* 39:301-312.

SAVAGE, S. (1945). A Catalogue of the Linnean Herbarium. London: Linn. Soc. London.

SEEMAN, B. (1863). The Solana of Tropical Polynesia. *J. Bot.* 1:206-211.

SEITHE-V. HOFF, A. (1962). Die Haararten der Gattung *Solanum* L. und ihre taxonomische Verwertung. *Bot. Jb.* 81, h.3:261-336.

SMALL, J. K. (1933). Manual of the Southeastern Flora. p. 1114. New York: Small.

SORIA, J. & HEISER, C. B. JR. (1961). A Statistical Study of Relationships of Certain Species of the *Solanum nigrum* complex. *Econ. Bot.* 15:245-255.

STAFLEU, F. A. (1967). Taxonomic Literature. Utrecht-Netherlands: International Bureau for Plant Taxonomy and Nomenclature. Zug-Switzerland: Inter-Documentation Co. AG.

STEBBINS, G. L. (1950). Variation and Evolution in Plants. 643pp. New York: Columbia University Press.

STEBBINS, G. L. & PADDOCK, E. F. (1949). The *Solanum nigrum* complex in Pacific North America. *Madrõno* 10:70-81.

SUTTON, A. W. (1909). Notes on some Wild Forms and Species of Tuber-bearing Solanums. *J. Linn. Soc. Bot.* 38:446-453.

SYMON, D. (1970). Dioecious Solanums. *Taxon* 19:909-910.

TANDON, S. L. & RAO, G. R. (1964). Cytogenetical Investigations in Relation to the Mechanism of Evolution in hexaploid *Solanum nigrum* L. *Nature* 201, 4926:1348-1349.

TANDON, S. L. & RAO, G. R. (1966). Biosystematics and Origins of the Indian tetraploid *Solanum nigrum* L. *Curr. Sci.* 20:524-525.

TANDON, S. L. & RAO, G. R. (1966) *in* Index to Plant Chromosome numbers for 1967 (1969). *Reg. Veg.* 59:90.

TURNER, F. (1898). The Supposed Poisonous Plants of Western Australia. Rep. 7th. Meet. Aust. Assoc. Ad. Sc. Sydney 1898:910-919.

VENKATESWARLU, J. & BHIRAVAMURTY, P. V. (1969). Morphology of the Pachytene Chromosomes of the Indian diploid *Solanum nigrum* L. *Genetica* 40:407-412.

VENKATESWARLU, J. & RAO, M. K. (1969). Chromosome Numerical Mosaicism in some Hybrids of the *Solanum nigrum* complex. *Genetica* 40:400-406

VENKATESWARLU, J. & RAO, M. K. (1972). Breeding System, Crossability Relationships and Isolating Mechanisms in the *Solanum nigrum* complex. *Cytologia* 37:317-326.

VILMORIN, R. DE & SIMONET, M. (1928), *in* DARLINGTON, C. B. & WYLIE, A. P. (1955). Chromosome Atlas of Flowering Plants. London: Allen & Unwin.

WARMKE, H. E. & OVERMAN, M. A. (1972). Cytoplasmic Male Sterility in *Sorghum*. *J. Hered.* 63(3):103-108.

WESSELY, I. (1960) ("1961"). De Mitteleuropäischen Sippen der Gattung *Solanum*, Sektion Morella. *Fedde. Rep.* 63:290-321.

WESTERGAARD, M. (1948), *in* DARLINGTON, C. B. & WYLIE, A. P. (1955). Chromosome Atlas of Flowering Plants. London: Allen & Unwin.

ZHUKOVA, P. G. (1967), *in* Index to Plant Chromosome Number for 1967 (1969). *Reg. Veg.* 59:74.

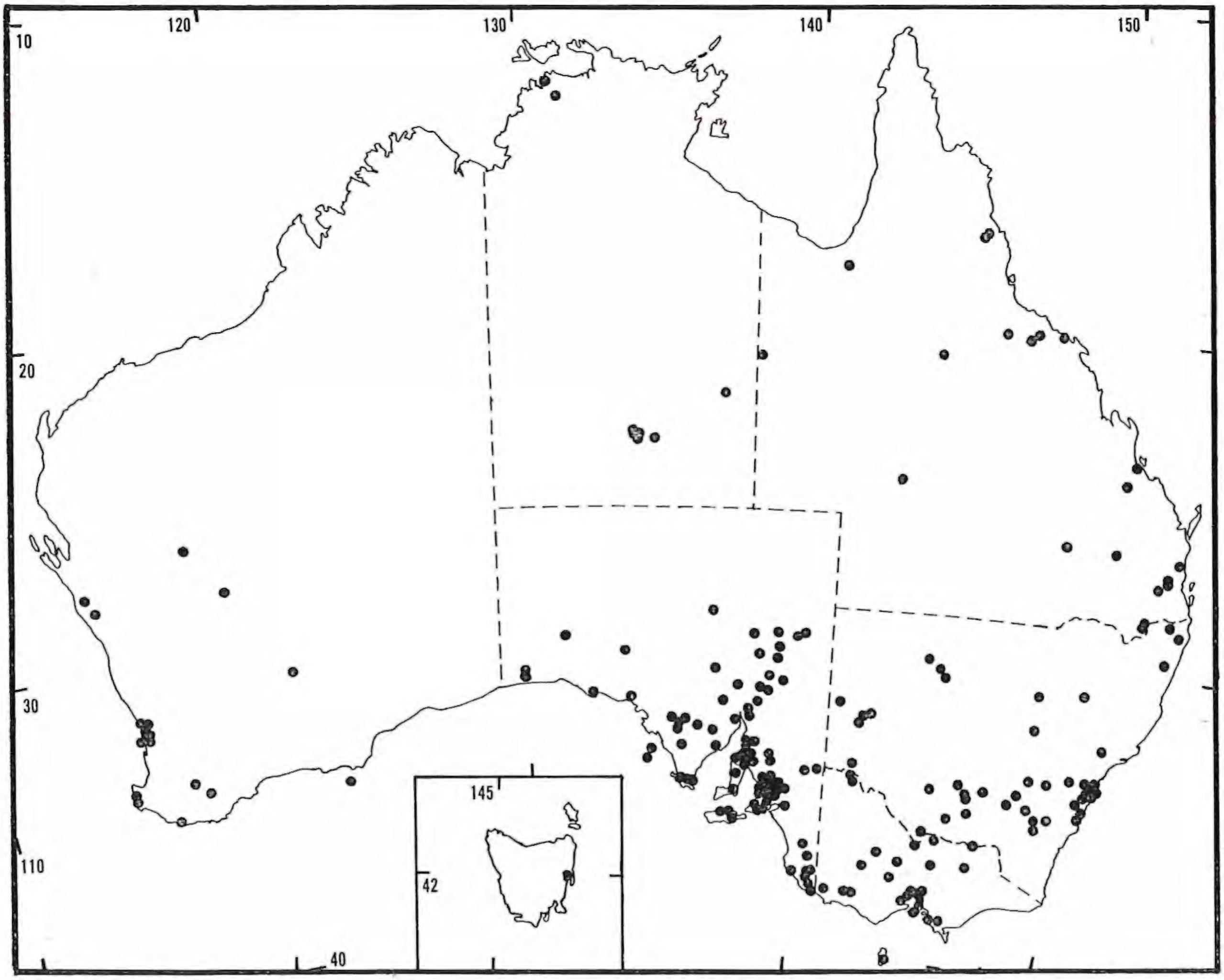


FIG. 2. Distribution of *Solanum nigrum* subsp. *nigrum* in Australia.

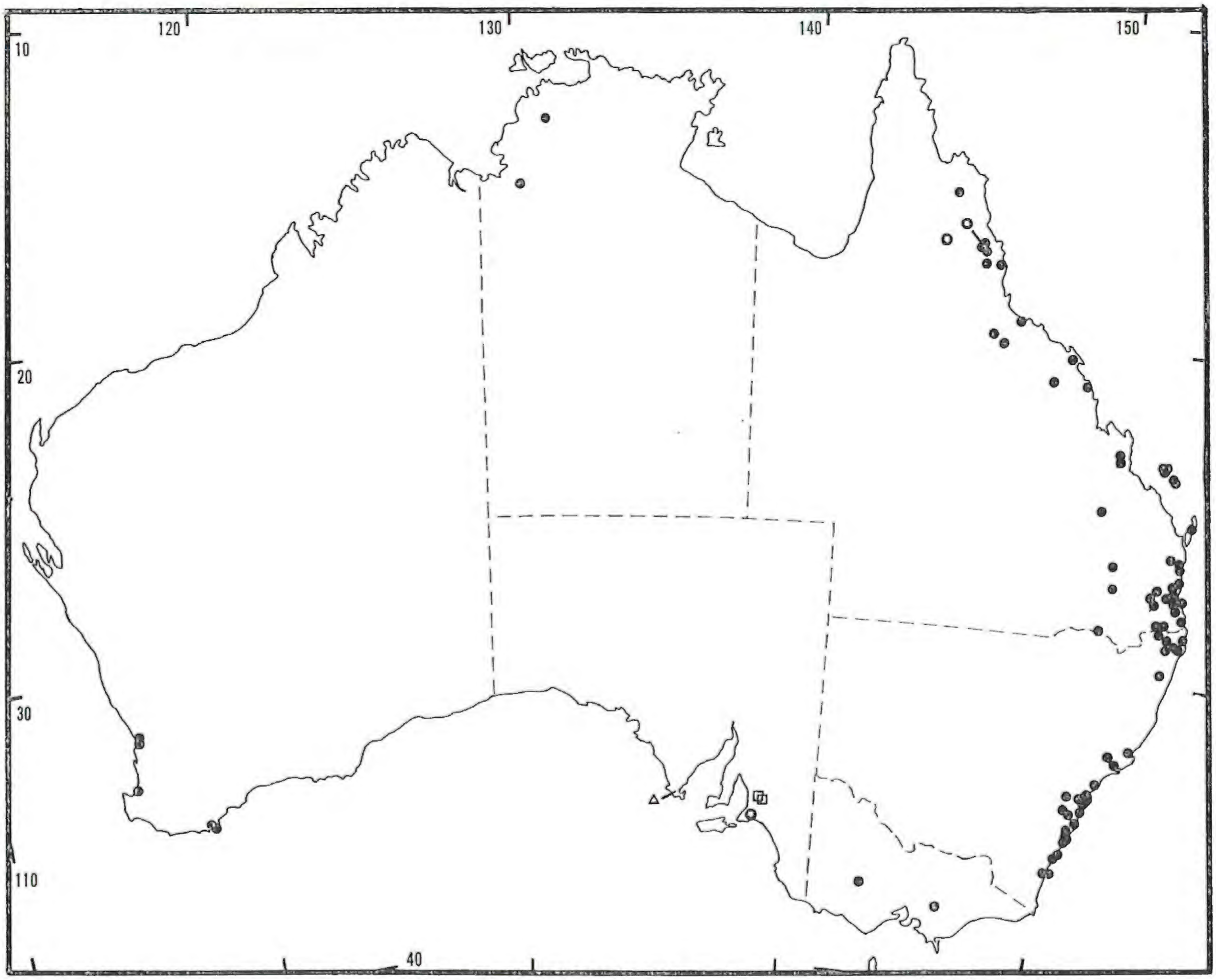


FIG. 3. Distribution of *Solanum nodiflorum* subsp. *nutans* (•), *S. nigrum* subsp. *schultesii* (□), *S. villosum* (o) *and S. retroflexum* (△) in Australia.

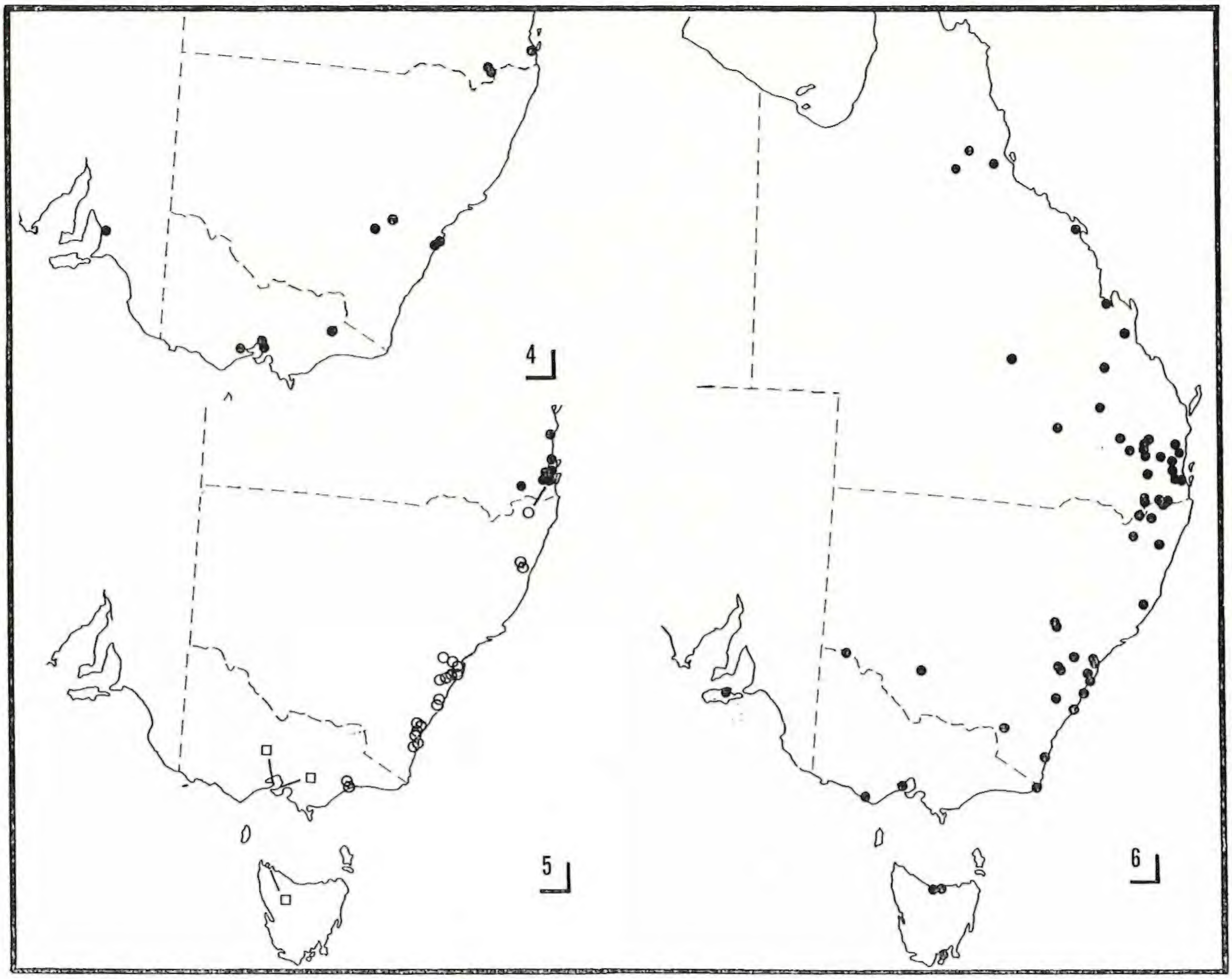


FIG. 4. Distribution of *Solanum nitidibaccatum* in Australia.

FIG. 5. Distribution of *Solanum nodiflorum* subsp. *nodiflorum* (●), *S. gracilius* (○), and *S. furcatum* (□) in Australia.

FIG. 6. Distribution of *Solanum opacum*.


PLATE 1. Lectotype of *Solanum nodiflorum* Jacq. Photographed by the British Museum (Nat. Hist.) Studio and published by permission; copyright remains the property of the Trustees of the British Museum (Nat. Hist.)

PLATE 2. Holotype of *Solanum nodiflorum* subsp. *nutans*.


PLATE 3. Lectotype of *Solanum americanum* Mill. Photographed by the British Museum (Nat. Hist.) Studio and published by permission; copyright remains the property of the Trustees of the British Museum (Nat. Hist.).


PLATE 4. Neotype of *Solanum opacum*.


PLATE 5. Lectotype of *Solanum scabrum* Mill. Photographed by the British Museum (Nat. Hist.) Studio and published by permission; copyright remains the property of the Trustees of the British Museum (Nat. Hist.).

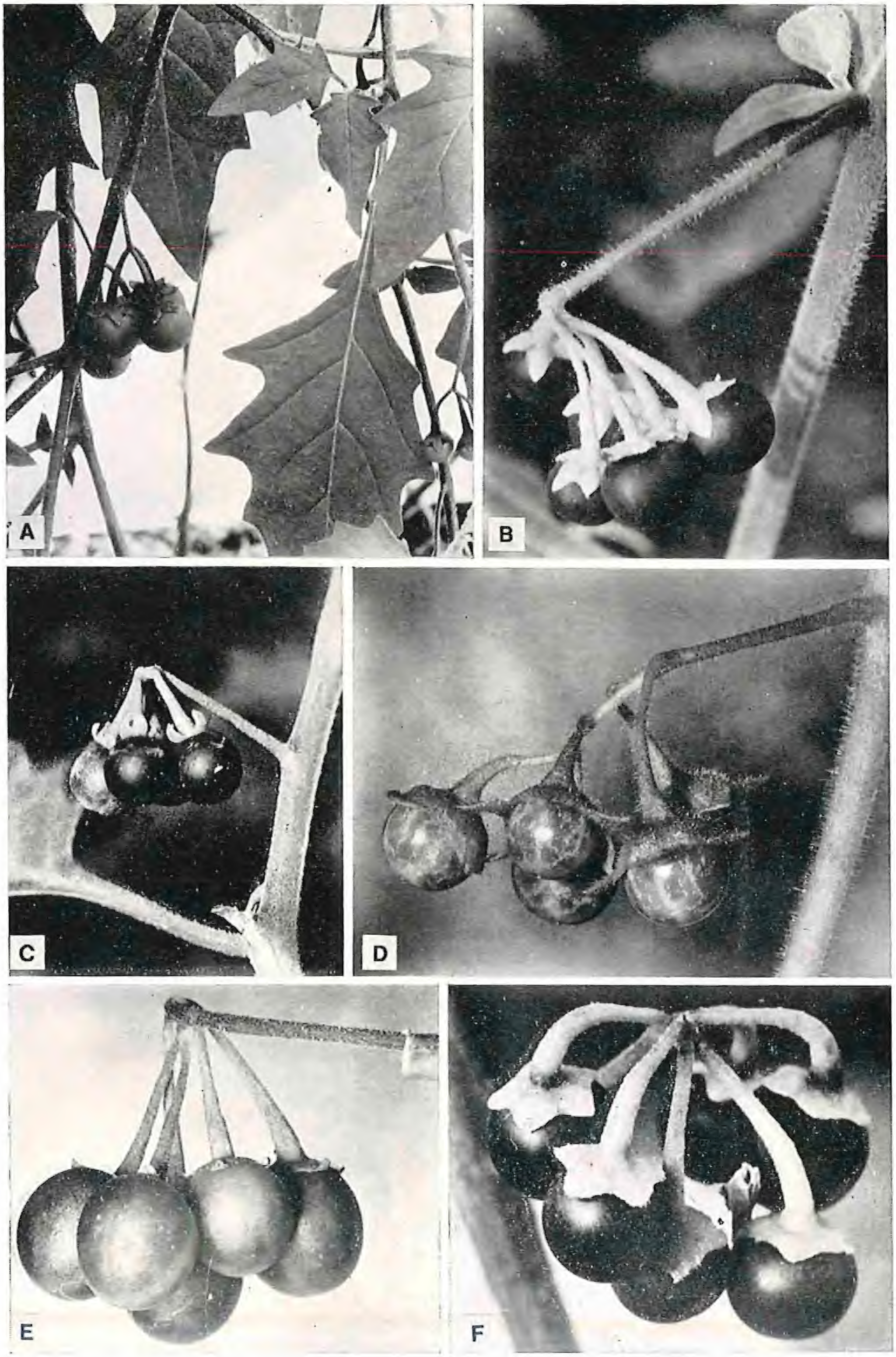


PLATE 6. Infructescences of species of *Solanum* sect. *Solanum* in Australia. (A) *S. opacum;* (B) *S. gracilius;* (C) *S. retroflexum;* (D) *S. nitidibaccatum;* (E) *S. villosum* (ex S. Aust.); (F) *S. nigrum* subsp. *nigrum*. All berries within the range 6-10 mm across.

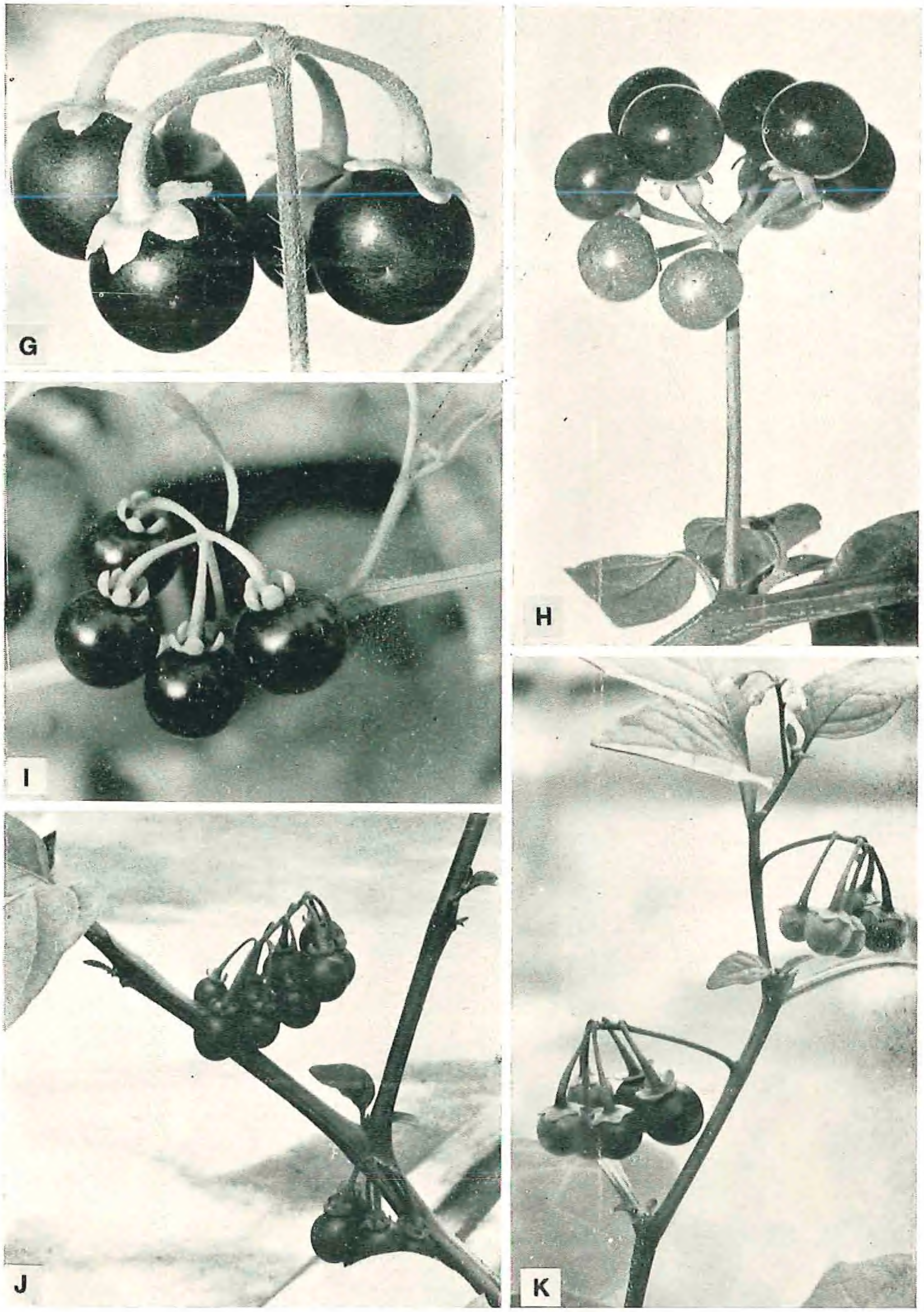


PLATE 7. Infructescences of species of *Solanum* sect. *Solanum* in Australia. (G) *S. nigrum* subsp. *schultesii;* (H) *S. nodiflorum* subsp. *nodiflorum;* (I) *S. nodiflorum* subsp. *nutans;* (J) *S. villosum* (ex n. Qd); (K) *S. nigrum* subsp. *nigrum* (seed ex N.Z.)—note racemiform infructescence typical of the species. All berries within the range 6-10 mm across.